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COMITÉ DE RÉDACTION

J. D. CARTHY, P. H. CHRISTENSEN, K. GÖSSWALD, P.-P. GRASSÉ,
C. JUCCI, A. RAIGNIER, T. C. SCHNEIRLA, T. UCHIDA

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1956

I

MÉMOIRES ORIGINAUX

STUDIES OF CASTE DIFFERENTIATION IN *MYRMICA RUBRA* L.
4. CONTROLLED LARVAL NUTRITION

by

M. V. BRIAN

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INTRODUCTION

In this paper it is proposed to consider the effects of controlling the nutrition of larvae that are fully competent to grow (that is that are taken from hibernating colonies in February or later) whilst all other culture conditions are normal. The diet was the same in all cases, and consisted simply in deprivation of all protein, leaving only water and sucrose; it was applied for varying periods at various stages of development (1) : first, permanently at various stages, and second, for various periods prior to growth (and hence at developmental stages that vary with the maturity of the larvae in winter-paper 3).

Such dietary control calls for some care as workers must not be able to lay eggs; hence prevernal types (those straight from hibernation) have been used, for these have had no access to protein since the autumn and are known not to lay (Brian, 1953). After 2 weeks there is a slight danger that they may start through mobilisation of fat-body protein reserves but fortunately periods of treatment as long as this have not proved necessary. In addition to this precaution larvae have been starved singly; for in groups if one dies the condition of all the others is suspect as it may either have been fed directly to them or after transformation into worker eggs. After dieting (when this preceded growth) the larvae were transferred (still single) to active vernal workers in normal culture conditions, and the usual ontogeny readings taken (paper 1).

(1) This is explained in the first paper of the series (Brian, 1954,)which is subsequently referred to as paper 1. Similarly the second and third contributions (Brian, 1955 *a* and *b* respectively) are referred to as papers 2 and 3.

Larvae can be kept alive for 20 days under these conditions and one has survived for 65 days, nevertheless few change very much after the eighth day. As the stage then reached is not far from the end of the A period, one may wonder whether it is the internal reserves that are used up, or whether segmentation needs some extra factor.

The positive evidence of this section that a sugar-rich proteinless diet favours worker generation is relevant to the hypothesis (advanced in paper 3) that rapid brood, which gives only workers, is produced through a similar, though of course less stringent, nutrition.

TABLE 2.

The average condition before and after dieting of female larvæ of various sizes and of male larvæ; using the brain positions as standard, the normal values of the other items have been inserted for comparison.

Class of larvæ.	Days.	Brain position.	Weight.		Leg area.		Wing area.	
			Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
16 large females	0	0.6	2.0	2.1	4.1	4	2.0	2
	9	0.8×	2.8×	3.3	7.9×	6+	2.5	4+
15 medium females	0	0.3	0.9	—	2.8	—	1.1	—
	14	0.6×	1.4×	—	5.2×	—	1.5	—
20 small females	0	0.1	0.5	—	1.7	—	0.6	—
	14	0.4×	0.7×	—	2.5	—	0.8	—
16 males	0	0.5	1.3	1.1	3.0	3	1.8	2
	14	0.7	1.8×	2.3	7.2×	5	6.0×	5

× a mean gain with $P < 0.01$.
+ the range of variation of this does not include the mean diet value.

Smaller female larvae.—Thirty-five individuals varying in weight from 0.3 to 1.4 mg. were treated for 14 days, a period more than sufficient to produce maximum change. For convenience of analysis they have been divided into two sub-groups based on initial size: one of 20 small ones (0.3 to 0.6 mg.) and one of larger ones (0.7 to 1.4 mg.) referred to henceforth as 'medium' ones. The mean values before and after treatment are given in table 2.

The brain position advanced 0.3 units in both the small and medium larvae. When it is realised that this is not statistically different from the figure of 0.2 for the largest of all, the evidence that the brain transit is size independant during this period of dieting is seen to be quite strong. This important property was of course one of the reasons (in another connexion) that it was chosen as an index of maturity (paper 1); the present result emphasises its suitability. But whereas all groups have

probably gained in maturity equally, they have gained in weight to a degree that varies with the initial size: by 0.8, 0.5 and 0.2 mg. from large to small respectively. The mean gains are significant ($P < 0.01$) but the interaction between gain and size is not quite (P slightly over 0.05) yet it may be taken to indicate a trend that is reasonable in view of the fact, recorded earlier, that the large larvae have far more reserve material in their trophocyte cytoplasm than the small ones. Leg area gains decreased in the same way: by 4,0, 2.4 and 0.8 units. In this case, the gain of the small larvae is not significant and the interaction between mean gain and size also falls short of the conventional level (P: 0.05-0.10). None of the gains in wing area are valid, and some of the smallest larvae gave no measurable increase at all.

Thus in essentials the smaller larvae react as do the largest and one may summarise by saying that this diet applied to female larvae after hibernation causes a size-independant maturation, a size-correlated gain in weight and in leg area, and no change in wing area. Neither the small nor the medium larvae showed increases in brain and leg sufficient to bring them into the state characterising the end of the A period, so that the question posed at the end of the previous section can be answered: a limit to change is set by an internal food reserve factor not by a fixed developmental stage; both may come into play in the largest larvae.

Male larvae.—Sixteen males were dieted for 14 days. Their mean brain position advanced by 0.2 units (Table 2), comparable with the female change, but in this case, owing to rather a large variation, not statistically significant. However, the weight, leg and wing increases are valid and the last especially worthy of note; the wing gained by at least 3 units in all 16 individuals, so that it is clear that in the male the wing is firmly geared to the growth schedule of the whole adult system—as it is in the female only after the 2-segment leg stage. As with the large females, the normal gain associated with a change of 0.2 units in the brain position has been shown in the table. Whilst the weight gain of the dieters is less than normal the leg and wing gains are more, although as in all three cases the values lie inside the normal's, range of variation too much weight should not perhaps be attached to this. It does, however, suggest that on the whole the adult system grows disproportionately to the total larval body—a result noted in the females in regard to their legs but not wings. Irrespective of sex, the dieting evidently causes an increase in the ratio of adult to larval systems; whereas in females the wings are excluded from this, in the males they do as the legs.

GROWTH AFTER DIETING

The largest female larvae.—Eleven larvae after full dieting treatment were cultured normally. All responded immediately and reached the segmentation period in a day. They took 3 days (in 3 cases), 4 days

(in 4 cases) and 5 days (in 4 cases) to segment. This rather wide variation is characteristic of worker-forming larvae in general in normal culture in spring from larvae of a variety of sizes; it contrasts with the behaviour of large larvae in October (paper 3) when periods of 2 or 3 days were the rule. More will be said about it later in this paper; meanwhile, it is evident that in no sense is the process of queen-potentiality destruction by dieting the converse of vernalisation; for not only are there visible changes in the dieting larvae, but their subsequent growth does not show the marked acceleration of maturation that characterises unvernalised individuals. Dieting forces the larva along a worker path to a point from which it cannot return; in other words it destroys the relatively unstable equilibrium of the queen-presumptive organism.

The average weight of the workers yielded was 4.3 mg., very near to the 4.4 mg. of October grown larvae (paper 3, Table 4).

Smaller female larvae.—These will be considered as previously in two size groups: small (0.3-0.6 mg.) and medium (0.7-1.4 mg.). The small ones did not all respond to food immediately, as they would have done if not starved (as far as is known from previous experience). Most delayed for from 4 to 6 days and a few longer still. Growth once started was pursued haltingly: in one extreme case a larva remained at the stage brain 0.8 for 25 days. On the whole the medium larvae showed less delay after being given food, and most had started to grow by the eighth day; once started they grew steadily. Out of the twenty small ones, 7 died: 5 in the B and 2 in the C period. Out of fifteen medium larvae 9 died: 5 in the A period and 4 in the B period. These variations may be taken to reflect a general deterioration of the organism through dieting; the medium larvae show, as would be expected, some intermediate features between small and large ones.

The segmentation period of the small larvae was normal: of 12 completing it, 5 had 4-day, 6 had 5-day and 1 a 7-day period. But the medium larvae produced a few short periods like those given by some of the largest larvae: of 10 that completed it, 2 had 3-day, 5 had 4-day, 2 had 5-day and 1 a 6-day period. C periods were normal. The adult weight was less than expected by normal culture: in particular 5 small larvae produced adults 0.6 mg. less than all but one previously known, and 5 medium ones produced larvae over 0.5 mg. less than any known before; yet, 12 of the small ones do not appear to have been affected by the treatment. In general the smaller larvae show reduced adult weight in about half the cases—in the large ones of course such occurs in all cases, as workers instead of queens result.

Male larvae.—Males responded for the most part immediately to food: of 13, 8 had gained more than 0.5 mg. by 2 days, 11 by 4 days and all by 6 days. This compares with females of similar size (medium), and contrasts with smaller females. Growth delays were common ; in the B period

especially only 2/13 gave the normal 5-day sequence; 7 gave 6-day, 2 gave 7-day and 2 gave 8-day periods. The C period was of 1 day (1 case), of 2-days (10 cases) and of 3 days (1 case) and so also longer on the average than normal (1.5 days). The weight after defecation shows no detectable correlation with the initial weight (as with normals) but in comparing the weights of dieted and normal adults, the precaution has been taken of comparing only those that come from the same initial weight range. Then the means are: 5.9 mg. (normal) and 4.7 mg. (dieted), a difference that is valid ($P < 0.01$). On the whole then, these males recall four of the five aberrant males (paper 2). They do not differ much from females of corresponding weight except in the important feature of not showing a reduced B period—one of less than 5 days. Unvernalised males can have 4-day periods which is a further indication, if one is needed, that pregrowth dieting is not the converse of vernalisation. The absence of even shorter B periods in males is no doubt due to the absence of a caste-differentiation process, as is the absence of wing independant growth and other effects characteristic of workers.

ONTOGENY DETAILS

With a view to gaining more knowledge of the caste-differentiation mechanism, an intensive study has been made of large larvae (> 1.5 mg.) that have been dieted for a period calculated to include that needed to destroy queen potentiality: 2, 3, and 4 days. Sixty-three larvae in 3 equal groups were used: the first (2 days diet) yielded 10 queens, 1 intercaste, 3 workers and 7 dead; the second (3 days diet) gave 5 queens, 3 intercastes, 9 workers and 4 dead; the third (4 days) gave 1 queen, no intercastes, 19 workers and 1 dead. Thus the required trend from queen to worker production was secured, and the expected normal proportion of intercastes (compare with 6/55 for normal material, paper 2) obtained.

As the variation between ontogenies of any one caste was no greater within than between the 3 diet-time classes, they have been grouped according to caste type as was done in the case of the study of progressive vernalisation. Using stage of maturity as a base, weights and wing areas (not leg areas for these behaved normally) have been averaged, and their full range of variation presented (in Tables 3, 4 and 5). Average growth rates, and maturation rates which necessarily involve time, have been calculated with origin not at the start of growth, as might perhaps be conventional, but about the middle: to be precise at the stage of transition from the A to the B period (the reasons for this have been explained in the earlier papers). Only compact distributions have been grouped and averaged; 2 unusual workers have been given separate treatment.

Table 3.

Weights and wing areas averaged per term of the standard maturity series for 16 queens produced from large larvæ after 2, 3 or 4 days starvation; also weights and maturity indices averaged day by day using the start of the B period as origin.

Standard Maturity Series.		Weight.			Wing Area.			Days from origin.	Daily mean Weight.	Daily mean maturity.
		Min.	Mean.	Max.	Min.	Mean.	Max.			
C	d	5.4	6.2	7.0		—				
	e	6.0	7.2	8.2		—				
	t	6.2	7.4	8.4		—				
								6	7.2	2.9
B	3	6.1	7.1	8.0	23	32	36	5	7.0	2.8
	2 ½	6.0	6.7	7.6	18	23	26	4	6.7	2.4
	2	5.6	6.3	7.2	13	17	21	3	6.2	1.9
	1 ½	4.7	5.5	6.7	11	13	16	2	5.5	1.5
	1	4.2	4.8	5.9	6	9	12	1	4.9	1.0
A	0.9	3.6	4.2	5.0	5	7	8	— 1	4.2	0.9
	0.8	2.9	3.3	4.2	2	5	7	— 2	3.4	0.8
	0.7	1.8	2.4	3.0	2	3	5	— 3	2.5	0.7
	0.6	1.5	2.1	2.6	2	2	3	— 4	2.1	0.6

The queens.—The rate of maturation of the queens was normal in the A period and in the first part of the B period, but after the 2-segment leg stage the average slackened off (last column of Table 3), for in 5/16 individuals two or three days elapsed instead of one between the 2- and the 3-segment leg stage, a retardation which accompanied a temporary cessation of growth. As a result these 5 gave 6 day B periods (in 3 cases) and 7 day ones (in 2 cases). In continuation of this trend, the longer C period (2 days) predominated (10/16 cases). This development retardation contrasts with the mild acceleration at the same stage shown by the semi-vernalised ones (paper 3, Table 8). Such a brief diapause at the stage of queen determination may be of great significance but no correlated features of weight or wing that might help in its understanding have been detected. It is reminiscent of the delay shown by the dieted males, except that it is more narrowly confined as regards stage of development; it may be no more than a caste-irrelevant response of the organism to dieting, but its absence before the 2-segment leg period in females suggests that the intercaste suppression process was intervening.

The specific growth rate is at first high, but declines continually in a way very like that of the semi-vernalised queens except that the actual average weight is a little less all the time (fig. 1). The weight/maturity relation calls for little comment as it resembles that of all previous queen

groups as far as the 2-segment leg stage, then it falls a little below due to the short diapause of some individuals (fig. 2). The adult size is only 0.2 mg. less than that of the *q* set (queens in February from small larvae),

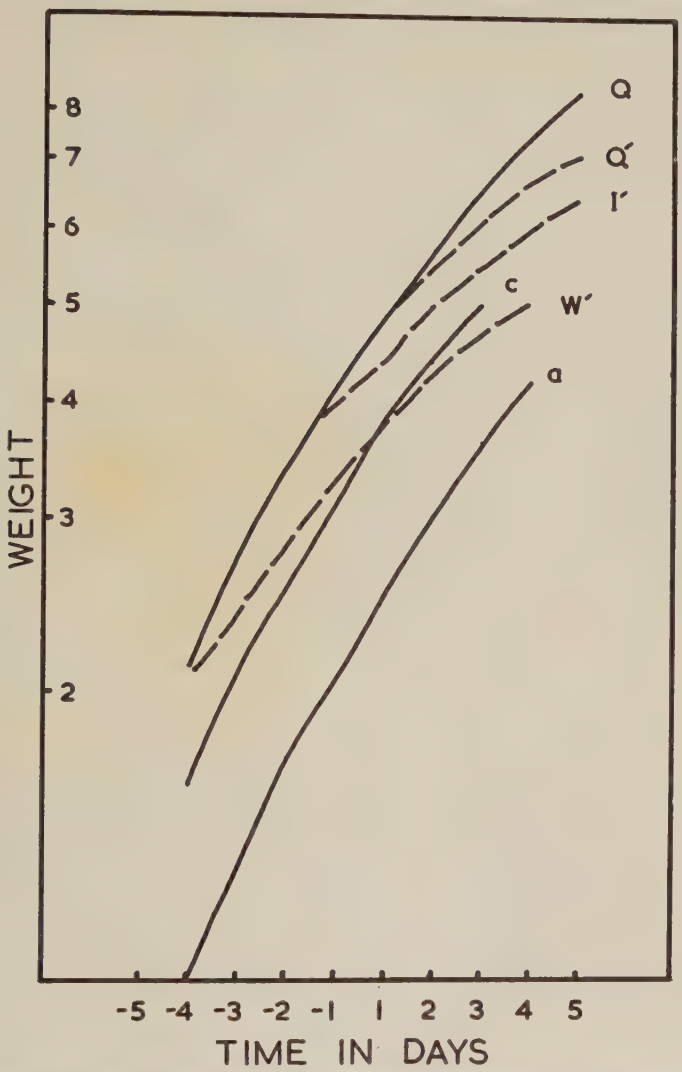


Fig. 1. — Average specific growth rates of pre-growth dieted queens (Q'), intercastes (I'), and workers (W') in broken lines ; with normal culture queens (Q). *c* and *a* type workers, in full lines, for comparison. Ordinate : weight on a log scale ; abscissa, time in days from an origin on the first day of the segmentation period.

certainly not a statistically significant difference. Wing growth is also normal.

The intercastes.—The largest intercaste (numbered 15 in continuation of the series) had an adult weight of 5.8 mg., ovaries of 8+8 ovarioles,

small lenses in all 3 ocelli, a moderately distinct post pronotal surture, but no wings, although in the larva at the 2 $^1/_2$-segment leg stage, their area was 21 units. Another (no. 16) weighed 5.7 mg., had ovaries of

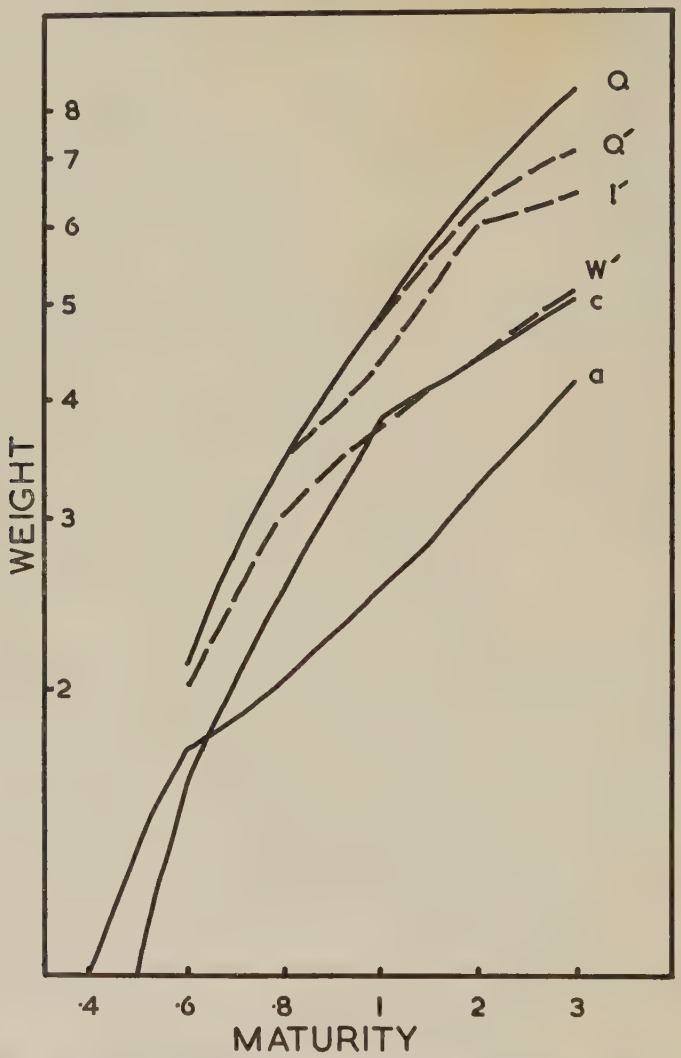


Fig. 2. — The mean paths of pre-growth dieted queens (Q′), intercastes (I′), and workers (W′) in broken lines ; with the normal culture paths of queens (Q), *c* and *a* type workers for comparison in full lines. Ordinate, weight on a log scale ; abscissa, the standard maturity series.

3+3 ovarioles, small lenses in all 3 ocelli, a good surture, and no wings, the maximum area in the larva being 16 units (at the 3-segment leg stage). A third (no. 17) weighed 5.3 mg., had ovaries of 2+2 ovarioles, small lenses in all 3 ocelli, an indistinct surture and no wings; the maximum larval wing was 12 units (at the 3-segment leg stage). Lastly an intercaste

(no. 18) weighed 5.1 mg., had ovaries of 2+1 ovarioles, very small lenses in the ocelli, no surture and no wings, the maximum wing area in the larva being 9 units (from the 1 $^1/_2$-segment leg stage onwards). One may note again the size correlation between larval wing and adult ovary.

Table 4.

Weights and wing areas averaged per term of the standard maturity series, for 4 intercastes produced from large larvæ after 2, 3 or 4 days starvation; also weights and maturity indices averaged day by day using the start of the B period as origin.

Standard Maturity Series.		Weight.			Wing Area.			Days from origin.	Daily mean Weight.	Daily mean maturity.
		Min.	Mean.	Max.	Min.	Mean.	Max.			
C	d	5.1	5.5	5.8						
	e	6.1	6.7	7.5						
	t	—	—	—						
B	3	6.0	6.5	7.2	9	16	21	5	6.4	2.8
	2 ½	5.9	6.2	7.0	9	14	18	4	6.0	2.5
	2	5.7	6.0	6.4	9	13	15	3	5.5	1.8
	1 ½	4.3	5.0	5.3	9	11	12	2	5.0	1.5
	1	3.7	4.4	4.9	7	9	10	1	4.4	1.0
A	0.9	3.7	4.0	4.4	—	—	—	— 1	4.0	0.9
	0.8	3.0	3.5	4.0	5	6	8	— 2	3.5	0.8
	0.7	1.9	2.7	3.8	—	—	—	— 3	2.6	0.7
	0.6	1.2	1.7	2.0	2	3	4	— 4	1.7	0.6

The maturation rate is normal in the A period and the early B period, but it then retards, as in the queens, from which in fact they hardly differ. The C period was of one day in all cases. The specific growth rate after a high initial value declined rather sharply 2 days before the end of the A period, and was less than that of the *q* queens until theirs declined too, in the B period (fig. 1); as a result the path (weight/maturity) fell below that of the queens at the start of the B period and remained there, although only 0.3 mg. less at the 2-segment leg stage (fig. 2). After this they gained on an average 0.5 instead of 0.8 mg. (with queens) up to the 3-segment leg stage. Thus the lower *average* weight of the intercastes (two weighing 5.7 and 5.8 mg. were heavier than the smallest queens) was due to growth rate deficiency rather than, as was the case on the whole with intercastes from the culture of semi-vernalised larvae, from excessive maturation rate. It may be recalled that the intercastes derived from normal culture (paper 2) were produced by a mixture of both causes.

The wing is the same as that of queens as far as the start of the B period when it falls away and is 4 units less on the average at the 2-segment leg stage (fig. 3). It only gains 3 units in the next stage of leg segmentation

as compared with 15 for queens. This is like the intercastes from semi-vernalised larvae, but unlike those from normal culture which were queen-like right as far as the 2-segment leg stage. It does not follow that they are determined as intercastes earlier than the normal culture ones (see later in this paper).

The workers.—The 31 workers included 2 that on the basis of all previous experience would have been expected to generate intercastes. They had wings of 10 units and weighed 5.5 mg. at the 2-segment leg stage and as such they occupied the fringe of the worker distribution of weights and wing areas, and overlapped those of the intercastes (Tables 6, 7 and 8). They are thus not distinct from the workers, but so extreme as to be worth special mention. Both had 4-day B periods.

TABLE 5.

Weights and wing areas averaged per term of the standard maturity series, for 29 workers produced from large larvæ after 2, 3 or 4 days starvation; also weights and maturity indices averaged day by day using the start of the B priod as origin.

	Standard Maturity Series.	Weight.			Wing Area.			Days from origin.	Daily mean Weight.	Daily mean maturity.
		Min.	Mean.	Max.	Min.	Mean.	Max.			
C	d	3.6	4.7	5.5						
	e	4.0	5.4	6.0						
	t		—							
B	3	4.2	5.1	6.0	3	5.0	10			
	2 ½	4.0	4.8	5.9				4	5.0	2.7
	2	3.7	4.4	5.4	3	4.9	7	3	4.7	2.3
	1 ½	3.5	4.0	5.0				2	4.3	1.6
	1	3.0	3.7	4.5	3	4.4	7	1	3.8	1.1
A	0.9	2.9	3.3	4.2				— 1	3.3	0.9
	0.8	1.8	3.0	3.8	2	3.6	4	— 2	2.8	0.8
	0.7	1.8	2.5	3.1				— 3	2.4	0.7
	0.6	1.6	2.0	2.4	2	2.2	3			

The remaining 29 workers have been averaged in one group (Table 5). The rate of maturation in the A period was the same as that of the other females, but in the B period it was substantially greater in most cases, the actual duration being 3 days (in 8 cases), 4 days (in 14 cases), 5 days (in 5 cases), 7 days (in 1 case) and 8 days (in 1 case). Thus although these larvae were not dieted until all change had ceased, they resemble those that were, in having a variable B period and both are in striking contrast to the mid-winter and October sets of cultures. The actual relative frequency of periods is quite similar to that of normally cultured ones of different initial sizes. The C periods were mostly short: of 1 day in 24 cases

and of 2 days in 5 cases; this again is a similar proportion to that of normals.

The average specific growth rate was at first high and even rose a little, but then, one day before the end of the A period it dropped to a slowly declining value less than that of the other females at each equivalent day (fig. 1). Their average adult weight, 4.7 mg. whilst larger than average, is identical with that of the *c* type workers and the mid-winter workers, and only slightly greater than that of October grown ones. In general, the workers from large larvae, no matter how they are produced, seem to have a very similar weight.

The combination of the high maturation rate and the low specific growth rate, produces a path (fig. 2) which diverges from the queen mode at the stage brain 0.8. In this aspect it is identical with the *d* workers and the *c* workers if their wing is considered rather than their weight, and with the mid-winter workers from large larvae. The simple generalisation that applied to intercastes: that mid-winter semi-vernalised ones resulted from development acceleration, that pretreated ones resulted from growth retardation and that normal ones resulted from a mixture of these two factors does not extend to workers without a little qualification. Whilst there certainly is growth retardation, there is also in most cases developmental acceleration, although not of the same degree as in unvernalised ones. It will be recalled that in the paper (no. 2) which considered normal workers, the length of the B period was found to have interesting associated features, which enabled it to be used as the basis of a natural classification of workers. When a similar subdivision is attempted with the present data, some interesting but different results emerge. Thus at the start of the B period, the average weights of the three groups with 3-, 4- and 5-day periods respectively are: 2.7, 2.8 and 2.8 mg., almost identical, and the average weights after defecation are 4.8, 4.6 and 4.6 mg., very much the same. It follows that the growth rate must have been inversely proportional to the B period duration or directly proportional to the maturation rate. In fact, an average weight of 5.0 mg. was reached after 3, 4 and 5 days by the three groups of that B period duration respectively. The biggest mean difference in weight occured on the third day, when the values 5.0, 4.7 and 4.6 mg. were recorded, but even these differences are not satistically significant.

The consequence of this positive association between maturation and growth rates is that all three groups follow the same path (fig. 2) but pass along it at different rates. This worker-characteristic g/d ratio which allows a wide variation in its component parts, is a new feature in such a restricted part of the ontogeny (the B period): its more general occurrence when the whole developmental period from winter larva to adult is considered has been commented on earlier (paper 2). The matter is reconsidered more generally in the discussion.

Little need be said of the wing area (fig. 3) : it ranged from 3 to 10 units at the 3-segment leg stage. This extension beyond the value 4 which

is the maximum in worker-generating smaller larvae appears, like the weight of adults, to be a feature of large larvae that produce workers, not only in the rare natural cases, but in the experimental ones as well.

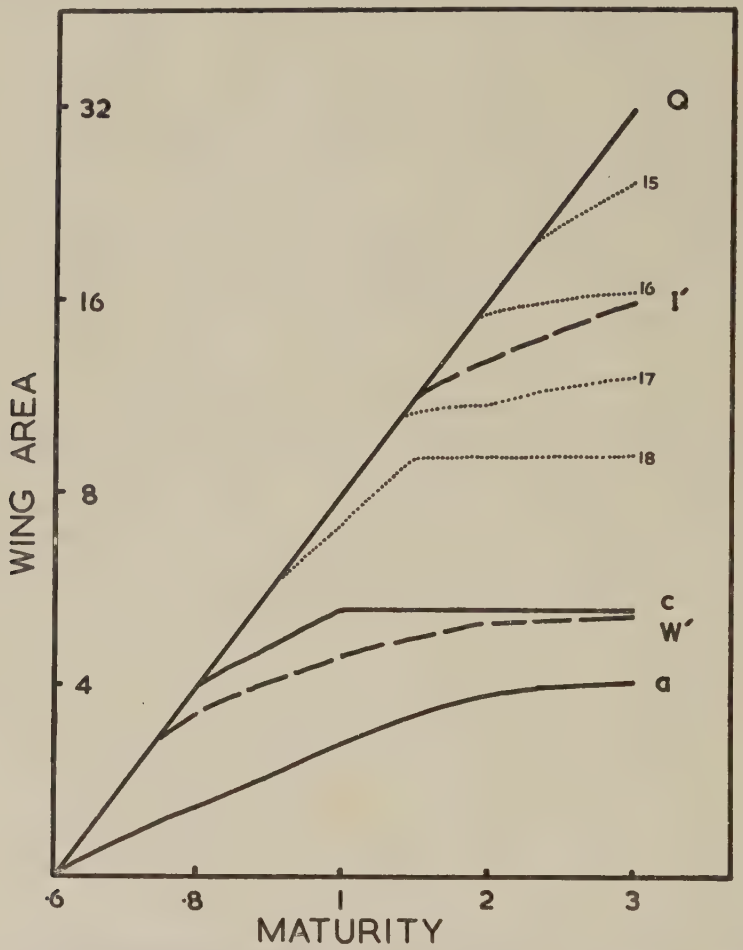


Fig. 3. — Average wing specific growth rates for pre-growth dieted intercastes (I′) and workers (W′) in broken lines ; with the normal wing growth of queens (Q), *c* and *a* type workers for comparison in full lines. The 4 intercastes (numbers 15-18) are marked individually as well. The experimental queens dit not differ materially from the normals and have not been marked separately. Ordinate, wing area on a log scale ; abscissa, standard maturity series.

Those dying.—Before concluding this section, a word must be said about those that died during growth, for the proportion is unusually high: 7/21 if only the first group is considered; 11/42 if the first two, and 12/63 if all 3 groups are considered. That the number dying is inversely proportional to the period of starvation indicates that it is not the starvation itself but some factor connected with the transition from one caste to the other. Confining attention to the large larvae (as defined) it can be ascertained that of 88 such, cultured by the same methods in October,

December, January and February, without pretreatment of any kind, only 7 died. In order to test the hypothesis that it is the critical period of 2 or 3 days that is responsible for the increase of mortality, namely the period of transfer from queen production to worker production, this figure should be compared with 11/42. When this is done, using the χ^2 test, a value of 7.27 with one degree of freedom and $P < 0.01$ is obtained. This then is the first time that mortality has intervened in a significant way in the breeding results (compare paper 2).

The animals died for the most part in the segmentation period; only one died during the pretreatment. The 11 others were last seen alive at the following stages and as the following presumptive adults: 1-segment leg (one queen), 1 $^1/_2$-segment leg (two queens and one worker), 2-segment leg (one intercaste and two workers), 2 $^1/_2$-segment leg (one worker), 3-segment leg (one intercaste), after defecation (two intercastes).

Although the proportion of intercastes is high (4/11), the fact that all the individuals are not intermediate (and this is the case even if the presumptive queens were really intercastes as they could have been) does not support the theory that the unusual mortality is due to some organic upset associated with the transition from the production of one caste to the production of the other. The matter must remain open for the time being.

FEMALE DIFFERENTIATION

The process of caste divergence in respect of wing area and weight may be considered by means of frequency tables for important stages of development, as in paper 2. By so doing, in as much as time is neglected and the rates of change of weight, wing and maturity (and their derivative quantities such as the g/d ratio) ignored, the step is a retrograde one; but it has two compensating features: that it invokes individual variation and, more important still, that it enables the female population to be considered as a whole (1). The general process is then as follows. At first the distribution is unimodal, and the two caste types (as they subsequently become) and the intercastes are randomly distributed within. The distribution then spreads out, and the caste-types become biassed and have different average values. Then a split develops and the population becomes bimodal and later perhaps quite divided. This last depends on the nature of the character chosen: with the wing which is perfectly discrete in the adults this happens, but with the weight which is not it does not happen—yet the weight is unexpectdly discrete at the stage immediately preceding queen determination.

The dispersion of the distribution may be due to purely random variation in growth rates (of weight and wing) and maturation rates, and so, internal caste bias may not be taken to indicate organic disparity. But the

(1) With the rate studies, only means and ranges were given. Whilst it is theoretically possible to include the individual variation as well by calculating as first differences between items of a series this is so complex as to obscure the essence of the situation, which is ably given by the mean.

development of a split may be so taken. Yet it is not necessarily the first sign of such disparity, for a marked bimodality of rate frequencies must have preceded it, and of this the means are the best indices: where a sudden deflection in a mean rate occurs it is quite reasonable to suppose that organic disparity exists (1).

At the end of the period of diet, there are certain differences between those larvae that later formed queens and those that later formed workers. The mean weights were: 2.13 mg. and 2.17 mg. respectively, both very similar; the mean brain positions were 0.61 and 0.69 respectively, again very similar and statistically probable ($P > 0.1$); the mean leg areas were 5.5 (queens) and 6.0 (workers) a difference with a statistically moderate probability (P: 0.05-0.10), but the mean wing was 3.1 (queens) and 2.6 (workers) a not very great but significant difference (P: 0.01-0.05). Thus as early as this, the wing-size is caste-biassed but within a wholly unimodal frequency distribution. It may be noted too, that the differences between the means of all four quantities indicate that those larvae that change least with the pretreatment are the ones to form queens—that is those that were most resistant to change, the most stable; they had smaller legs, larger wings, smaller bodies and were less mature.

TABLE 6.

Wing area and weight frequency distributions at stage brain 0.8, for normally cultured (February), unvernalised (October to mid-January) and pre-treated (2-4 days of proteinless incubation in February) females.

		NORMAL.				UNVERNALISED.				PRE-TREATED.			
		W	I	Q	S	W	I	Q	S	W	I	Q	S
Wing Area	1	2			2								
	2	10	1		11	1			1	1		1	2
	3	12	—	2	14	16	3	10	29	13		—	13
	4	2	3	8	13	9	3	2	14	13		8	21
	5	1	1	6	8	1	1	2	4	4	2	5	11
	6		—	5	5		1	2	3		1	1	2
	7		1		1						—	1	1
	8										1		1
Weight classes	1.0 —	1			1								
	1.4 —	5			5								
	1.8 —	8	1		9					2			2
	2.2 —	7	1	2	10	1			1	4		1	5
	2.6 —	4	3	5	12	3	1		4	7		2	9
	3.0 —	1	1	9	11	9	3	2	14	10	2	5	17
	3.4 —	1		2	3	8	2	6	16	7	1	4	12
	3.8 —			2	2	4	1	4	9	1	—	3	4
	4.2 —			1	1	2	1	4	7		1	1	2

W, workers; I, intercastes; Q, queens; S, sum.

(1) Bimodality although theoretically definable is in practice not so easily detected; moreover there can be chance bimodality.

In the Tables 6-8, the weight and wing frequencies have been set out for the three development stages: brain 0.8, 1-segment leg and 2-segment leg; in addition to the females discussed in this paper those of the three previous papers have been included, condensed into three categories: queens, intercastes and workers. Altogether 156 females are involved: 85 workers, 18 intercastes and 53 queens. This is not, of course, an unbiassed sample of the growing population, on the contrary it is the result of various deliberate attempts to upset the caste differentiation mechanism.

The wing data will be considered first, as it gives better discrimination (as was pointed out apropos of normal culture larvae in paper 2—with

Table 7.

Wing and weight frequency distributions at stage 1-segment leg for normally cultured (February), unvernalised (October to mid-January) and pre-treated (2-4 days of proteinless incubation in February) females.

		Normal.				Unvernalised.				Pre-treated.			
		W	I	Q	S	W	I	Q	S	W	I	Q	S
Wing Area	2	5			5								
	3	9			9	9			9	4			4
	4	10			10	14			14	17			17
	5	1			1	3		5	4	7			7
	6	2	1	1	4	—	1	—	1	2		1	3
	7		1	1	2	1	4	1	6	1	1	—	2
	8		—	6	6		1	3	4		—	1	1
	9		—	3	3		2	4	6		1	5	6
	10		2	4	6			2	2		2	3	5
	11		1	4	5			3	3			4	4
	12		1	2	3			2	2			2	2
Weight classes	1.4 —	3			3								
	1.8 —	3			3								
	2.2 —	8			8								
	2.6 —	4			4	1			1				
	3.0 —	3			3	4			4	4			4
	3.4 —	2	1	2	5	8			8	11	1		12
	3.8 —	3	—	1	4	4	2		6	10	1		11
	4.2 —	1	2	4	7	6	3	1	10	5	—	3	8
	4.6 —		2	6	8	3	3	6	12	—	2	7	9
	5.0 —		1	7	8	1		4	5	1		3	4
	5.4 —			1	1			3	3			2	2
	5.8 —							1	1			1	1
	6.2 —							—	—				
	6.6 —							1	1				

W, workers; I, intercastes; Q, queens; S, sum.

the exception of the intercastes). At the stage brain 0.8, the total female distributions are unimodal and with only slight internal caste bias, but at the start of the B period they are bimodal with marked caste bias. Thus there is no doubt that the divergence between workers and queens can be traced back to brain 0.9 by this method. This must result from the rather sharp change in path at brain 0.8, which indicates that this is probably the stage when dissecting influences first start. In general then, all three sets of data agree in pointing to the A period as one in which certain sub-standard females (small stature, low specific growth, rate, small wing) are fixed or determined as workers (for no cases of reversion to the queen type of development are known).

TABLE 8.

Wing and weight frequency distributions at stage 2-segment leg for normally cultured (February), unvernalised (October to mid-January) and pre-treated (2-4 days of proteinless incubation in February) females.

		Normal.				Unvernalised.				Pre-treated.			
		W	I	Q	S	W	I	Q	S	W	I	Q	S
Wing Area classes	1 —	2			2								
	3 —	22			22	23			23	17			17
	5 —	3			3	3			3	9			9
	7 —				—	1			1	3			3
	9 —				—		3		3	2	1		3
	11 —		1	1	2		1		1		1		1
	13 —		—	—	—		2	2	4		—	1	1
	15 —		4	8	12		1	8	9		2	4	6
	17 —		1	6	7		1	3	4			5	5
	19 —			5	5			1	1			5	5
	21 —			1	1			2	2			1	1
Weight classes	2.2 —	1			1								
	2.6 —	5			5								
	3.0 —	7			7								
	3.4 —	7			7	6			6	2			2
	3.8 —	2			2	5			5	9			9
	4.2 —	3			3	5			5	6			6
	4.6 —	2			2	8			8	7			7
	5.0 —		2		2	2	1		3	4			4
	5.4 —		4	1	5	1	4	1	6	3	1	3	7
	5.8 —			6	6		2	5	7		2	3	5
	6.2 —			8	8		1	3	4		1	9	10
	6.6 —			5	5			5	5			—	—
	7.0 —			—	—			1	1			1	1
	7.4 —			1	1			1	1				

W, workers; I, intercastes; Q, queens; S, sum.

By the 2-segment leg stage, the wing distributions are discrete (as between the workers on the one hand and the rest of the females on the other—except for the two diet anomalies). The intercastes which here share a unimodal but internally biassed distribution with the queens separate from them between this and the 3-segment leg stage in all the material. Even later in development these differences are further emphasised through the growth of the wing in queens during the transformation stages (C period, prepupa and pupa).

The data for weight agrees with that for the wing in essentials, but differs in detail. At the stage brain 0.8, the distributions are unimodal and almost imperceptibly caste-biassed. At the start of the B period they are still unimodal however, although clearly internally caste-biassed. But by the 2-segment leg stage bimodality is obvious and there is only a slight overlap of the caste types; the intercastes are on the whole with the queens rather than the workers. This distinction blurs in all three sets at the 3-segment leg stage and again later.

GENERAL CONCLUSIONS

At this stage it is convenient to review the principal facts that have emerged from this study (published in papers 1-4 inclusive) and to suggest a simple deterministic explanation. First it was shown that third instar larvae were caste-plastic after winter. Then the ontogenies of various sorts of individuals were studied and a maturity series established that is a sequence of qualitative changes in the body, independant of size, and though necessarily sequential, of time as well. The gradual transit of the brain from the cephalic capsule into the prothorax was found suitable in the first part of the instar, and after that the stages in segmentation of the leg buds of the adult embryo. These buds grow during the phase of brain transit, then segment, and finally transform into their adult shapes and positions (during the C period as it has been called, the prepupa and the pupa).

The ontogeny data in addition to the maturity series consisted of the leg-bud area, and the wing-bud area and the weight. The leg area provides an index of the rate of growth of the embryo adult, the wing of the degree of caste dimorphism and the weight of the degree of caste difference in size. To review the results generally, a group of larvae (females), may be considered from the time they enter the third instar until they are pupae. First consider them as far as the stage brain 0.5, that is when the brain is half way into the prothorax, for this is an important stage when diapause supervenes in some cases.

At the start they vary in size and their future depends not only on this but on the time of year, for both temperature and worker action (both have been shown to be relevant) vary seasonally. If they are amongst the first larvae in a season they will grow uninterruptedly and form workers

(rapid brood) but the ontogenies of these have not yet been investigated sufficiently to say more than this. If they enter the third instar rather later, they undergo a period of diapause at the stage mentioned, but if they enter the instar later still in the year, they only grow as opportunity allows before the winter, resuming in spring, and passing the stage brain 0.5 without any diapause. Although the larvae have various sizes, and grow at various rates, and may or may not have diapaused, there is no evidence that any caste division exists, and the female population, though variable, appears homogeneous.

The second half of the A period (brain 0.5 to 1.0) is that in which worker ontogenies deviate from queen ones. It is possible that this sensitive period really ends at the stage brain 0.8 for the evidence of the two last papers has indicated that this is a more important stage than was earlier thought (the *c* type workers whose maturation rate undoubtedly changed as late as brain 1.0 *did* show signs of a reduction of wing growth rate at the earlier stage). Larvae that attain to this period during the summer (excluding the rapid ones) grow very slowly (secondary diapause) at a high ratio of maturation rate to specific growth rate and never pass beyond the stage brain 0.8. They remain during autumn and winter and form the 'large' class. If forced to grow artificially they deviate from the queen mode at the stage brain 0.8 (to form workers) or later (to form intercastes). After winter all larvae grow quickly through this period, many deviating, particularly those that were small and less mature than brain 0.5 during winter. The results suggest that deviation is not diffuse, but concentrated at two stages: brain 0.6 (the *a* and *b* types) and brain 0.8 (the *c* and *d* types and the mid-winter and dieted types from large larvae). The *e* type probably deviate between brain 0.5 and 0.6 but this is not very clear at the moment. The later deviants form rather larger workers on the average, and it is quite a possibility that these two modal stages of deviation have in the evolution of the higher Formicidae become more distinct, and separated by greater size differences than in *Myrmica* where there is no evidence of polymorphic workers when the populations are considered as a whole.

Deviation consists of a reduction of the ratio of specific growth rate to maturation rate at about the same time as a reduction in the specific growth rate of the wing (and no doubt of other caste-differential features). In most cases the reduction is brought about by an increase of maturation rate compared to that of queens but in some cases (the *d* workers and the workers with 5-day B periods among the dieted set) it is due to a reduction in the specific growth rate without a corresponding reduction in rate of maturation (although this is also reduced to some extent). The reduction of the remarkably constant queen-type specific growth rate of the wings is not always quite simultaneous with the general physiological change; thus in normal culture intercastes, the wing changed later than, and in normal culture workers of the *c* type earlier than, the g/d reduction. Once deviation has occured, no reversion appears to be possible.

This period then is one of form-instability in which, what must be presumed to be a delicate equilibrium between the larval and the adult system, is easily upset and a different but stable equilibrium established (worker determination). Whilst it is undoubtedly true to say that the deviant process is a neotenic one in the sense that isomeric growth ceases and certain organs slow and stop growing altogether, it is not quite correct to say that their form is fixed in the juvenile state, for the ovary at least undergoes transformations (but not partitioning) that fit it for a functional existence in the adult worker: it is neoteny within the framework of a holometabolous life-cycle. The worker may reasonably be conceived, with these reservations, as an adult female whose wings and ovaries (and other features) have been fixed in the state they were in when the organism first left its queen-generating state of equilibrium.

The factors that increase the chances of deviation appear to be : small stature, weak growth (whether due to debility or lack of food), small wing and, in fact, general subnormality. Experimentally, two principal methods have been used. First by culturing large presumptive queen-forming larvae in autumn: they show very poor growth potential and develop very quickly with the adult system obviously dominant. As winter passes they acquire a greater power of sustaining growth, so that first intercastes and then larger and larger queens are produced. There are no visible changes in the larvae during vernalisation and it is probably a process of physiological change which leads to a gradual reactivation of a growth promoting gland. Secondly, by dieting fully vernalised large larvae on sugar and water, before normal culture: they put on a little weight only, and develop on a typical anisomeric manner. The greater the degree of distortion of the adult embryo produced by these means the less the subsequent chance of queen formation. On being transferred to normal culture these larvae show one singularity: they all develop at the same average g/d ratio but at very different rates, some growing and maturing quickly, others slowly.

During the diet of sugar and water the larvae are undoubtedly drawing on their reserve protein for the construction of the leg buds. They are in effect getting a sugar-rich assimilable protein diet: and this appears to resemble that which Weir (unpublished) has shown is given by vernal workers to second instar larvae and which converts them into rapid brood. There are thus two lines of evidence at least that a diet rich in sugar favours worker formation. The question naturally arises whether the workers are able by controlling the diet to influence the caste of these post-winter larvae. If they have this power they do not appear to use it in an arbitrary manner : for it is fairly easy to predict the fate of a larva if its culture conditions are known. Although they might give more protein to large larvae (and they certainly give more food even in proportion to their relative weights to these), it is difficult to conceive all the workers agreeing on a 95 % precise division of the larvae into queen-and worker-destined groups—intercastes would be expected to be more

frequent than in fact they are. Rather the evidence points to the fact that if workers do control caste via the diet of the larvae they do it in collaboration with them: such as for example if the deviation of a larva from the queen mode of growth was accompanied by a change of signal that led to a change in worker attitude. But until this is established fact it seems preferable, even though the theory is less attractive to sociologists, to suppose that the change lies entirely with the larva which may perhaps either select only sugar after worker determination has taken place rejecting (at any rate insoluble) protein, or, failing even this degree of control, eat what it is given of a normal menu and regulate its caste internally by a purely physiological mechanism.

An interesting feature about the deviation from presumptive queen ontogeny type is that the later it occurs the more severe is the reduction of the g/d ratio, and the less severe is the reduction of the wing specific growth rate. The result of the first is that there is a general convergence towards a unimodal worker size, a characteristic that contributes towards the size-bimodality of the general female population. This regulative feature can be given a rational deterministic explanation if the larva is regarded as a dual organism (as it has been repeatedly in this series) composed of larval and adult systems, the former acting as a food absorber, and the latter 'feeding' off a portion of this. If this is allowed, it is reasonable to suppose that the greater the power of the larval system (perhaps a function of its size, perhaps acting through a hormone intermediary) the greater the rate of growth of the whole double organism; and conversely the greater the power (again probably a function of size) of the adult system the greater the rate of maturation of the combine. Whilst eventually the adult comes to occupy the whole, it is quite likely that for a long period of early development the two systems maintain an equilibrium (of varying stability) and that the ratio of power is in favour of the larval system in the queen presumptive individuals and of the adult system in the worker determined ones. If one assumes for simplicity that there is a queen characteristic ratio of larval/adult systems and a lesser ratio characteristic of workers, it follows that the ultimate size of the adult queen must be greater than that of the adult worker, and that the approach to this end must be by way of a high g/d ratio for queens and a low one for workers—as has in fact been shown. But the low g/d ratio of workers is only an average feature, and the longer they develop as queens the greater is the adjustment that has to be made after deviation—one may visualise the adult system absorbing the surplus larval system and growing and maturing quickly. Hence the later a deviation occurs the greater the path deflection that results. Those workers that are determined early in ontogeny by contrast would carry a balanced pair of systems, in which the food absorbed by the larval component would be immediately transferred (in part) to the adult component, and as the larval system would thus be small, the general growth rate would be low.

This theory may also accommodate the fact that wings show more

momentum the later they deviate from the queen mode of specific growth. It is only necessary to add the notion that the adult embryonic parts compete for the absorbed solutes that are available and that there is a dominance order of success (to use the sociologist's terminology) headed by the ventral members—the leg buds in particular—and with the wing and ovary at the bottom of the scale. In those individuals that deviate late, the wing would be expected to continue growing whilst the adjustment of equilibrium was taking place, for it is assumed that there is then an abundance of food; its rate would of course slow down and eventually stop as the legs and other ventral parts attain complete dominance over the reduced food supply.

One other point may be considered. It has been shown that protein deprivation of large larvae leads to a transfer of reserves to the growing legs of the adult embryo (up to a limit). The rate of liberation of this reserve is likely to be low, and it is not surprising that the wings and ovaries at the bottom of the dominance order are unable to obtain any of it. After 2-4 days of this, the larvae would be in a variable state: some might have become completely adjusted to the worker value of the ratio of adult to larval systems; others might have only just lost their queen equilibrium. The former type would be expected to grow and develop slowly (the 5-day B period ones), whilst the latter would be expected to behave as *c* type workers in which the adult system was quickly adjusting itself to the fact of worker determination. In the former the growth rate would be higher than in the latter because of the larger larval system but it would last for less time. As a result the same path is taken by all types but at rates which are a function (one supposes by this theory) of the size of the larval system at the time of switch to normal culture.

In the segmentation period, to resume the survey of larval ontogeny in the third instar, it is necessary to examine a dual larval population consisting of worker-determined forms and queen presumptive (but not determined) forms. Beyond emphasising that the former are in fully stable equilibrium nothing need be added to what has already been said.

The non-worker females continue to grow isomerically without any elaboration until the 2-segment stage when their ovary has rudimentary partitions. Those that deviate in the period prior to this show some queen characters in the adult, but not all—perhaps because the size of the organ influences the form it can adopt—thus it was noticed earlier that the size of the germarium probably affects the number of ovarioles that can be formed. In addition to this there is the fact that deviation at this stage means even less reduction of growth rate of the wing than at earlier stages: it has 'momentum'. For these reasons it is not appropriate to regard the individual as being fixed in the deviation form, rather it is its potentialities for differentiation or perhaps more strictly elaboration that are hampered. Deviation in this stage is far more common amongst semi-vernalised large larvae than any others (except those starved artificially) and as these are the ones that lack strong growth it seems that with

the restoration of the potentiality for this during winter, there also develops a mechanism for assessing female quality and accelerating development in sub-standard ones. Either the assessment process whatever it may be, or the acceleration process appears to act more effectively when there is a higher growth potential. Up to the 2-segment leg stage, may be regarded as a period of growth of the caste-differential organs in addition to that shown by worker determined individuals that enables them to elaborate into forms of queen type; although it is not a period of extra growth in body size, since it takes place at a higher g/d ratio than in workers it does lead to a greater body size in the adult. The organism, although in a more stable equilibrium, is not fully stable and deviation although rare does occur and with resultant intercastes. Viewed in another way, the assessment mechanism even in spring is not absolutely perfect, and some individuals that have not the power to sustain growth or develop slowly enough are passed through.

This period of transition to the queen organ pattern is an obvious target for evolutionary action given that intercastes are socially disadvantageous. If it could be made fully stable—and one way would be to perfect the assessment mechanism—so that there was a sharp change from instability (the worker determination period) to stability (the queen formation period) then it would be possible to extend it and so obtain a bigger difference in caste mean size. But unless stability is first obtained, the proportion of intercastes would be increased. A further avenue for evolutionary progress that has already been mentioned in an earlier paper (no. 2) is in a subdivision of the sensitive period for worker fixation; the rather diffuse but suggestively double period of *Myrmica* might be accentuated so that several worker sizes could result.

The male requires only brief mention. It has a simple single ontogeny-type, and varies only slightly in its rate of growth, rate of maturation and ultimate size, and of course it shows no neoteny, no anisomeric growth, no polymorphism, and no size-bimodality. It is non-diapausing and non-vernalising, both of which in different ways have been shown to bear on caste production. Whilst the proportion of the adult to the larval system is increased by dieting the shape of the adult system remains unchanged. There is no reason to suppose that it differs in any way from a normal insect—the process is perfectly sex-linked.

Here, at the conclusion of this series of papers on caste differentiation, I should like to express my appreciation of the stimulating encouragement and generosity that Professor C. M. Yonge, F.R.S., C.B.E., has continually shown towards this work. It was largely done in his department at Glasgow.

Summary.

Large queen-potential third instar larvae after winter have been cultured with sugar and water, but no protein, for various times at various stages.

When presumptive queens are treated permanently in the pre-segmenttation period they die: but if treated in the segmentation period they yield either intercastes, if they were of 2-segment leg stage of maturity or less at the time dieting started, or queens if more mature.

When treated before post-winter growth they show a small increase in maturity (size-independent as far as one can tell) and an incommensurate gain in weight, but a more than commensurate gain in leg area (both greater in larger larvae) and no gain in wing area. In male larvae the adult system also gains at the expense of the larval but the wing grows with the leg. Subsequent growth under normal conditions is often sporadic, with higher mortality and smaller adults than usual; only in some females from large larvae is there an acceleration of development in the segmentation period.

Details of the ontogenies of queens, intercastes (which are not abnormally frequent) and workers derived from large larvae pre-treated for a period covering that known to be critical for the destruction of queen-potentiality are given in the usual way. The main features are: some queens show a short delay in development just after determination; the intercastes result from growth failures; the workers result from growth failure late in the A period and varying degrees of development acceleration in the segmentation period.

A comparison of these ontogenies with those given in earlier papers is made, and the results of all contributions to date summarised.

Resumen.

Durante varios tiempos y etapas después del invierno la larva en estado final reina-potencial grande se ha tratado con azúcar y agua pero no con proteina.

Cuando las reinas presuntas se tratan permanentemente en el periodo de pre-segmentación, ellas mueren. Si se tratan en el período de segmentación producen cruzadas, si hubiesen llegado a desarrollar patas hasta 2-segmentos/o menos al comenzar la dieta, o reinas si fuesen más avanzadas.

Cuando se tratan antes del crecimiento post-invernal, demuestran un pequeño aumento de madurez (tanto se puede apreciar, el tamaño no depende de ello) y un desproporcionado aumento de peso. Pero más que proporcionado en las patas (estos aumentos mayores en la larva grande) y ningun aumento en las alas.

Asimismo, en los machos, el sistema adulto crece a expensa del larval pero las alas crecen con las patas. Subsecuente crecimiento bajo condiciones normales, es frecuentemente irregular, con mayor mortalidad y adultos mas pequenos que de costumbre. Solo en algunas hembras de lava grande se encuentra un desarrollo acelerado durante el periodo de segmentación.

Detalles de la ontongene de reinas, cruzadas (cuya frecuencia no es anormal) y trabajadoras derivadas de larva grande tratadas anteriormente

por un período cubriendo aquel conocido como crítico para la destruccion de potencialidad de reina, se dan en la manera de costumbre. Puntos principales son : Algunas reinas demuestran una pequeña demora en su desarrollo siguiendo su determinación. Las cruzadas resultan por falta de desarrollo. Las trabajadoras son resultado de esta falta en la ultima parte del período A y distintos grados de aceleración de desarrollo en el periodo de segmentación.

Se ha efectuado una comparación de estas ontogenes con aquellas anteriormente producidas asicomo tambien un resumen de toda contribución recibida a la fecha.

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LE CYCLE DE DÉVELOPPEMENT DES CASTES CHEZ *RETICULITERMES*

Par

Harro BUCHLI

Les jeunes imagos ailés des Termites apparaissent régulièrement une fois par an. Chez la majorité des espèces, on connaît la date de leurs essaimages. Ainsi le *Reticulitermes lucifugus* et sa sous-espèce le *Reticulitermes l. santonensis* produisent des essaims une fois par an aux mois de mars, avril ou mai, selon les conditions climatiques du printemps. L'essaimage peut se faire en une seule fois ou en plusieurs lots, à des intervalles d'un à plusieurs jours. Les jeunes imagos quittent leur colonie maternelle de préférence après une pluie, pendant une matinée bien ensoleillée entre 9 heures du matin et 1 heure de l'après-midi.

Le fait que les imagos apparaissent tous au même moment dans une colonie laisse supposer que la production des nymphes, futurs imagos, est cyclique.

Nous avons déjà écrit (1956 *a* et *b*) que les nymphes de *Reticulitermes* parcourent huit stades de l'œuf jusqu'à l'imago, dont deux larvaires et six nymphaux, l'imago apparaissant au neuvième stade. Ce développement peut se faire en cinq à six mois chez le *R. l. santonensis* et en six à sept mois chez le *R. lucifugus* commun lorsque la colonie se trouve à une température constante de 25° C. Dans la nature, où les bassses températures de l'hiver freinent ou arrêtent tout développement, cette évolution nécessite cependant douze mois.

L'observation de colonies élevées au laboratoire et un grand nombre de prélèvements chez des colonies naturelles ont montré que la composition d'une colonie change selon la saison et que les nymphes se trouvent toujours presque toutes au même stade.

Ainsi les colonies ne possèdent que peu d'œufs et de larves en hiver, mais contiennent une importante quantité de grandes nymphes, fait également observé par Grassi et Sandias en Italie (1893-1894), outre les ouvriers, les sexués et les soldats dont se compose normalement la colonie. Tout développement de la colonie est bloqué pendant cette saison.

Au début du printemps les nymphes de l'avant dernier et septième stade se transforment en nymphes du dernier stade à longs fourreaux alaires. A cette époque, il n'y a que rarement des jeunes individus de cette caste dans la colonie.

A partir du moment où les nymphes subissent la mue imaginale jusqu'à quelques semaines après l'essaimage des jeunes imagos ailés on assiste à la ponte d'une grande quantité d'œufs. Les larves qui sont issues de cette ponte massive donnent en majorité (65 à 95 %) des jeunes nymphes à partir du troisième stade. Cette caste apparaît donc en masse au début de l'été.

En dehors de cette période relativement courte, le nombre d'œufs pondus est plus faible et les larves deviennent toutes, à peu d'exceptions près, des ouvriers, dont quelques-uns se transforment en soldats.

Les jeunes nymphes parcourent rapidement pendant l'été les premiers stades nymphaux et atteignent pour la plupart l'avant dernier ou même le dernier stade en automne, avant que la basse température hivernale ne vienne arrêter leur développement.

Une colonie de *Reticulitermes lucifugus* soumise aux conditions climatiques normales pour le sud et le sud-ouest de la France voit donc son rythme de ponte, la destinée des larves, les rapports numériques entre les castes subir une évolution cyclique au cours d'une année. Il existe un *cycle biologique* annuel au terme duquel la colonie se libère par un essaimage printannier des jeunes imagos formés au cours de l'année écoulée.

Nos observations ont cependant montré que chez le *Reticulitermes l. santonensis* ce cycle annuel peut se transformer en un *cycle semestriel* lorsque les colonies sont placées dans des conditions de milieu optima constantes.

A La Rochelle nous avons constaté que certaines colonies produisent deux essaims presque chaque année. Ceci vraisemblablement parce qu'elles habitent dans des maisons bien chauffées pendant la saison froide. Ainsi les nymphes formées après l'essaimage du printemps essaiment en automne de la même année à l'intérieur de la maison, même s'il fait mauvais temps dehors.

En voici deux exemples caractéristiques :

ESSAIMAGES D'IMAGOS DE RETICULITERMES A LA ROCHELLE

Colonie A.

Cette colonie s'est installée dans une maison isolée dans un grand jardin. Les essaimages ont en partie été observés et notés par le propriétaire, M. Roturier, et en partie par l'auteur.

Essaimage du 25 mars 1950 : imagos sortent d'un trou creusé dans le plâtre d'un mur de la cuisine, vers midi. Le mur est ensoleillé. Journée belle et chaude.

Essaimage du 10 octobre 1950 : le chauffage est en marche depuis trois semaines. Les imagos sortent d'un trou dans le plâtre, derrière un radiateur du salon, vers midi. Journée froide, mais ensoleillée.

Essaimage du 15 mars 1951 : les imagos sortent du trou dans le plâtre, derrière le radiateur du salon, à 16 h. 20. Journée belle mais froide.

Essaimage du 18 mars 1951 : les imagos sortent d'une poutre du plafond de la cuisine à 11 heures. Temps froid et pluvieux.

Colonie B.

Cette colonie, qui semble très grande, est installée dans une maison construite en briques et ciment. Celle-ci est attaquée jusqu'aux poutres de la toiture. Les observations ont été faites par les propriétaires.

Essaimage du 11 mai 1950 : les imagos sortent vers 1 heure de l'après-midi d'un trou creusé dans le ciment du mur extérieur, face sud-ouest, environ 3 m au-dessus du sol. Temps beau et chaud.

Essaimage du 12 octobre 1950 : la maison est chauffée. Les imagos sortent en haut d'un encadrement d'une porte de cuisine, vers 17 heures. Temps froid et pluvieux.

Essaimage du 24 février 1951 : les imagos sortent d'un trou creusé dans le plâtre, au-dessus d'un radiateur d'une pièce voisine de la cuisine vers 18 heures. Temps froid et pluvieux.

Essaimage du 19 mars 1951 : les imagos sortent de l'encadrement de la porte de la cuisine vers 14 heures. Temps froid et couvert.

Essaimage du 14 avril 1951 : les imagos sortent du trou dans le mur extérieur vers 17 heures. Temps beau et chaud.

Dans un des deux cas, des essaimages identiques se produisent encore aujourd'hui. Notons qu'il y a cependant dans la colonie B un essaimage au mois de février, c'est-à-dire quatre mois après l'essaimage automnal. Il se compose, nous semble-t-il, d'individus retardés appartenant apparemment au même lot que ceux ayant essaimé en automne.

Chez le *Reticulitermes lucifugus* commun, qui semble, selon des observations récentes, avoir un développement plus lent (le dernier stade nymphal étant plus long), nous n'avons jamais pu observer la transformation du cycle annuel en cycle semestriel.

Herfs (1951) semble cependant avoir observé des cycles semestriels dans des colonies de *Reticulitermes lucifugus* italien tenues dans des chambres à température constante. Hagen (1855) observe deux essaimages par an en Italie, Banks et Snyder (1920) font des observations analogues chez le *Reticulitermes virginicus* et le *Reticulitermes tibialis* en Amérique.

Toutes ces données indiquent donc que le cycle annuel peut être modifié.

ESSAI D'INTERPRÉTATION :

Nul doute que les facteurs à l'origine de l'évolution cyclique des castes sont extrêmement complexes. Il nous semble cependant que les conditions du milieu d'une part et le facteur alimentaire, auquel nous nous sommes souvent référé dans nos travaux antérieurs (1956 *b*), d'autre part, jouent un rôle des plus importants.

Comme nous avons pu le constater chez les sexués imaginaux de colo-

nies primaires, élevés dans la nature, les femelles ne pondent pas pendant l'hiver, mais accumulent pendant cet arrêt d'activité des matières de réserve considérables et deviennent très grosses. La ponte se déclenche au printemps un peu avant l'essaimage. Les sexuées sont alors particulièrement fécondes et une grande masse d'œufs et de larves apparaissent dans les colonies.

Après l'essaimage des jeunes ailés, la colonie se trouve dans des conditions de milieu extrêmement favorables. L'humidité et la température créent généralement un milieu optimum vers la fin du printemps. Le potentiel alimentaire est alors élevé, surtout aussi grâce à la disparition du grand nombre de nymphes qui, auparavant, devaient être nourries. Cette suralimentation de la colonie semble être la *conditio sine qua non* de la transformation en nymphes des larves issues de cette masse d'œufs.

Une alimentation qualitativement et quantitativement abondante semble, selon nos observations et essais, être responsable de la transformation des larves en nymphes. Cette manière de voir est appuyée par le fait que des colonies placées dans de mauvaises conditions (manque d'ouvriers nourrices ou de nourriture) sont inaptes à fournir des nymphes et des imagos.

Lorsque dans une colonie le nombre de nymphes est devenu élevé, la destinée de la plupart des larves qui éclosent est changé et elles donnent des ouvriers. D'après nos observations, ceci est principalement dû à l'abaissement du potentiel nutritif de la colonie, qui se voit obligée de nourrir les nombreuses nymphes présentes.

Dans le cas du cycle semestriel, les essaimages du printemps et d'automne sont moins importants. Ceci se comprend parce que les sexuées ne peuvent plus accumuler des réserves de corps gras durant l'hiver et sont alors moins fécondes, au temps des essaimages. Mais, puisque les conditions du milieu sont favorables dans une maison bien chauffée, les nymphes arrivent à l'état imaginal en cinq à six mois et peuvent alors essaimer en automne ; toutefois les imagos n'arriveront généralement pas à la fondation de nouvelles colonies. Dès que le lot des nymphes a quitté la colonie maternelle, le potentiel nutritif de celle-ci augmente et les œufs pondus en automne pourront se développer en larves sans arrêt hivernal puis en nymphes et puis en un nouveau lot d'imagos ailés, qui quitteront la colonie au printemps.

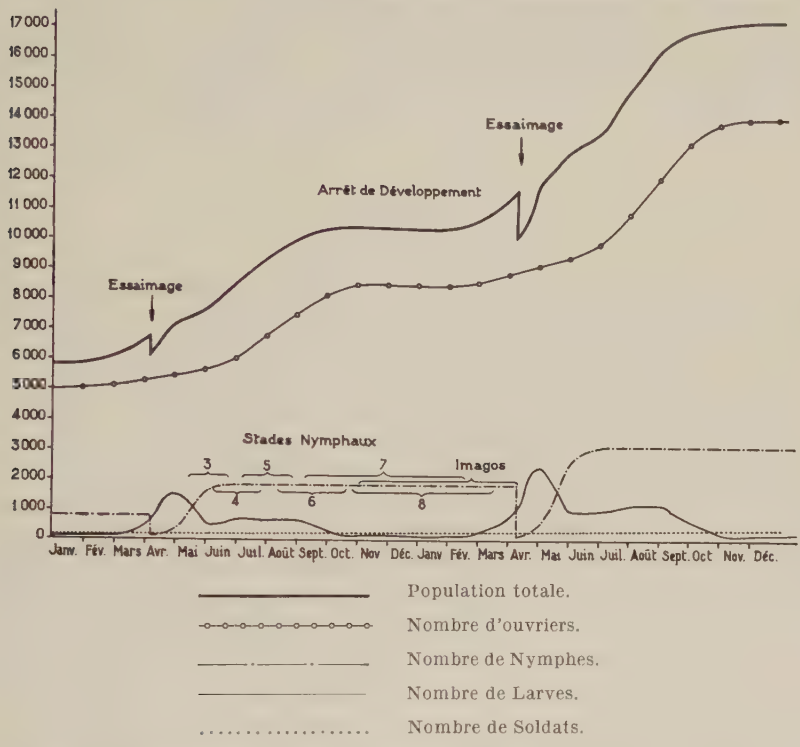
Ajoutons encore que l'observation de colonies tenues en chambre à température constante nous a montré qu'un tel régime finit généralement par dérégler la productivité de la colonie, à tel point qu'il y a, à tout moment, un petit nombre de nymphes et de temps en temps des imagos dans le nid, sans que des essaimages se produisent.

L'importance des variations climatiques se montre d'ailleurs aussi chez les autres espèces de Termites.

Dans la nature, le *Calotermes flavicollis*, spécialement étudié par Grassé (1942, 1952) et Grassé et Noirot (1945), produit des essaims en août et en septembre, et l'évolution de la colonie s'opère suivant un cycle

annuel, si la durée des stades qu'a donnée Harvey (1946) est correcte. En maintenant des colonies à une température constante on peut provoquer l'apparition d'imagos ailés pendant toute l'année. Ils essaiment alors en petits groupes de deux ou trois individus quelle que soit la saison.

S'il est facile d'obtenir des imagos dans des colonies de Termites infé-



Les courbes montrent pour chaque caste la croissance numérique. Le nombre de nymphes et de larves, ainsi que leur présence dans la colonie, changent rythmiquement selon la saison.

Les chiffres sur lesquels s'appuient ces courbes sont hypothétiques. Il est impossible d'ouvrir un nid et de compter les représentants de chaque caste d'une grande colonie, sans détruire ainsi son équilibre social et son développement normal. Pour cette raison, les courbes n'ont qu'une valeur relative, qui se base sur de multiples observations de différents colonies pendant les quatre saisons de l'année.

Ajoutons encore que le nombre de sexués fonctionnels du type néoténique augmente d'une année à l'autre dans les colonies de *Reticulitermes*. Pour cette raison, une population de cette espèce s'accroît très rapidement.

rieurs, cela est dû au fait qu'il y a moins de coordination et interdépendance sociale. Comme Grassé et Noirot l'ont mis en évidence, les nymphes peuvent, en effet, s'alimenter de bois et devenir des imagos sans dépendre du potentiel alimentaire d'une véritable caste nourricière.

Chez les Termites supérieurs, où, d'après Grassé (1949) et Noirot (1949, 50, 51, 52), dans beaucoup de cas les larves venant d'éclore paraissent dès le premier stade être déterminées soit pour la lignée des nymphes soit pour celle des ouvriers, le cycle annuel de développement des castes nous

paraît être soumis aux mêmes facteurs extérieurs. Chez *Nasutitermes matangensis* et chez *Macrotermes gilvus* les essaimages se produisent au début de la saison des pluies. Bathellier (1927) constate que c'est aussi en ce temps où l'humidité et la température sont optima qu'apparaissent les nymphes. Pendant la saison sèche, les larves ne donnent par contre que des ouvriers. Si les larves sont vraiment déterminées dès qu'elles éclosent, cela n'annule pas, nous semble-t-il, l'importance du facteur alimentaire. La valeur du potentiel alimentaire peut en ce cas influencer indirectement le sort des larves, par l'intermédiaire de la reine de la colonie, qui peut selon son alimentation produire des œufs plus ou moins riches en vitellus.

Résumé.

La production des castes, notamment des nymphes, futurs imagos ailés et des ouvriers chez le *Reticulitermes lucifugus* est soumise à un cycle biologique annuel. L'auteur montre que dans les colonies naturelles les nymphes apparaissent quelques semaines après l'essaimage des jeunes imagos, vers la fin du printemps en une fois et en grande quantité. Elles se développent pendant l'été et arrivent en automne à l'avant-dernier ou même au dernier stade avant la mue imaginale. En hiver le développement de la colonie est normalement arrêté par le froid. Au début du printemps les nymphes se transforment en imagos et quittent la colonie. Pendant le repos hivernal les sexuées femelles accumulent beaucoup de corps gras et, au moment où les grandes nymphes se transforment en imagos, une ponte massive se produit dans le nid. Après la disparition des imagos la colonie voit son potentiel nutritif considérablement augmenté, puisqu'il n'y a plus de nymphes à nourrir. Pour cette raison les larves, à leur tour bien alimentées, peuvent se transformer en nymphes. Celles-ci, par leur croissance et leur constant besoin de nourriture, abaissent de nouveau le potentiel alimentaire. En conséquence de cette baisse, les larves qui apparaissent pendant l'été et l'automne sont mal nourries et donnent des ouvriers.

Si les colonies de *Reticulitermes l. santonensis* ont leur nid dans une maison bien chauffée en hiver, comme c'est le cas dans quelques immeubles de La Rochelle, le *cycle annuel* peut se transformer en *cycle semestriel*. Les nymphes formées au printemps arrivent à l'état imaginal en automne et essaiment alors. Quand ils quittent la colonie un nouveau cycle commence qui permet un autre essaimage cinq à six mois plus tard, au printemps.

L'auteur suppose que le facteur climatique et le facteur alimentaire jouent le rôle principal dans la formation des nymphes et dans le cycle biologique des Termitières.

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ÜBER ZENTRIFUGIERVERSUCHE AN FORMICIDEN

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Vorstand: Prof. Dr. Gößwald

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A. — EINLEITUNG

1. — ALLGEMEINES

Die Zähigkeit und Widerstandsfähigkeit der Ameisenimagines sowohl Umwelteinflüssen als auch anatomischen Eingriffen gegenüber, ließ die Frage aufkommen, wie sich Ameisen der Einwirkung der Zentrifugalkraft gegenüber verhalten. Auch Larven und Puppen wurden zu den Untersuchungen herangezogen. Hier interessierten vor allem die Fragen, welcher Art die zu erwartenden Defekte sein werden und auf welche Weise sich die Ergebnisse mit denen von Guareschi (1934 *a*, 1934 *b*, 1934 *c*, 1936) vergleichen lassen werden.

Dem Experimentieren mit Ameisenlarven und -puppen stehen zum Teil erhebliche Schwierigkeiten entgegen. Das liegt einmal daran, daß der Larvenkörper infolge einer starken Turgeszenz im Körperinnern, Epidermisverletzungen gegenüber sehr empfindlich ist ; die sofort heraustretende Lymphe ist selten aufzuhalten und bedingt fast immer das Absterben des Objektes. Zum anderen werden auf Grund der sozialen Instinkte der Arbeiterinnen die behandelten Larven und Puppen, die wieder ins Versuchsnest zurück müssen, meistens als fremd erkannt und getötet. Ein isoliertes Aufwachsen von Ameisenbrut ist nur kurze Zeit möglich.

Vorliegende Arbeit führte ich auf Anregung meines verehrten Lehrers, Herrn Prof. Dr. Gößwald, am Institut für Angewandte Zoologie der Universität Würzburg in den Jahren 1949 bis 1951 aus. Herrn Prof. Gößwald bin ich für wertvolle Hilfe, dem chemischen Institut für die Benützung der elektrischen Zentrifuge sehr zu Dank verpflichtet.

2. — METHODE UND TECHNISCHES

Zentrifugiert wurde mit einer elektrischen Zentrifuge, die für bestimmte Umdrehungszahlen genau determinierte Fixpunkte hatte (Maximaltourenzahl 3600 U/Min.). Um orientiert zentrifugieren zu können, schob ich in die Zentrifugengläschen Pappstreifen ein, die an ihrem Ende einen Paraffinaufsatz hatten. Dieser paßte sich der konischen Gläschenform genau an. Im Paraffin wurde ein kleines Rechteck so ausgehoben, daß gerade Raum für die zu zentrifugierende Ameise war. Die Glaswand diente als Deckel ; ein Verrutschen des Objektes war völlig ausgeschlossen. Die Zentrifugengläschen konnten durch Abschneiden oder Hinzufügen von Paraffin an den Aufsatz genau tariert werden, so daß durch die gleiche Belastung ein ruhiger Lauf gewährleistet wurde. Längeres Arbeiten mit hoher Tourenzahl wurde vermieden, da die Temperatur im Inneren rasch ansteigt ; nach Schmidt-Ries (1926) bei 3500 U/Min. nach 15 Minuten um 15° C ! — Das Paraffin wurde in Parallelversuchen auch durch Holundermarkklötzchen ersetzt.

Zentrifugiert wurde orientiert und unorientiert. Im ersten Falle versuchte ich Unterschiede zwischen Zentrifugation in Kopflage (Kopf zentrifugalwärts gerichtet) und Abdominallage (Abdomen zentrifugalwärts gerichtet) zu ermitteln.

Für histologische Untersuchungen wurden die behandelten Objekte zum Teil sofort nach dem Zentrifugieren, zum Teil nach einiger Zeit erst fixiert.

Angewandt wurde das von mir (1951, 1954) und anderen Autoren erwähnte und gut bewährte Fixiergemisch nach Carl (Mansour, 1927). Bei Geschlechtstierbrut (bes. Puppen) stellten sich jedoch sonderbare Ausnahmen ein : trotz Hitzefixierung begann sich jedes Objekt innerhalb der folgenden Minuten derart zu strecken, daß gerade das Charakteristische nach der Zentrifugierung, das durch die Sedimentationswirkung hervorgerufene Zusammenrutschen, verloren ging. Dadurch wurden die Puppen fast 1 1/2 mal so lang als sie „normal" waren. Hier befriedigte also das Carlsche Gemisch nicht. Dieses Strecken der fixierten Puppen trat ebenfalls bei Anwendung anderer Fixiergemische ein : Carnoy, Susa, Petrunkewitsch (alle kalt oder warm angewendet). Als völlig ungeeignet für Geschlechtstierfixation erwiesen sich die Gemische nach Zenker, Helly, Maximow u. ä., wenn sie kalt angewendet wurden; besser waren die Resultate bei 24stündiger Einwirkung 40° C heißer Gemische. Überraschend gut wurden die Mißstände durch Anwendung von schwach mit Aqua dest. verdünntem Formol (38 %ig) bei 60° C behoben (2stündige Einwirkung). Auch durch eine Modifizierung des Carlschen Gemisches (größere Formolzugabe bei längerer Hitzeeinwirkung) gelang es mir, die Streckung der Puppen weitgehend zu verhindern und eine gute Durchfixierung zu erzielen. Wichtig ist, für langes und gründliches Entwässern mit absolutem Alkohol sowie für langes Entspriten mit Methylbenzoat (bis zu zwei Wochen bei mehrmaligem Wechsel) zu sorgen.

Bei ausgefärbten Puppen sowie bei Imagines schaltete ich anfangs zur Chitinerweichung Diaphanol dazwischen und behandelte anschließend mit einem Gemisch einer 5%igen Natriumnitrat- und 2,5%igen Natriumthiosulfatlösung. Dieses Verfahren hatte jedoch viele Nachteile, und ich konnte es umgehen, indem ich die Objekte so lange wie möglich (über 2 Wochen) in Methylbenzoat liegen ließ.

Gewöhnlich benutzte ich die Methode über Alkohol-Methylbenzoat-Benzol-Paraffin ; um in gewissen Fällen beim Schneiden ganz sicher zu gehen, wendete ich die Celloidin-Paraffinmethode nach Pfuhl an (für Formiciden in den Zeiten modifiziert), die über Alkohol-Aether-Alkohol-Celloidin 2%ig-Celloidin 4%ig-Chloroform-Carbolbenzol-Benzol-Paraffin geht. Das Aufziehen der Schnitte durfte nach dieser Methode nicht mit

Aqua dest. (sog. japanische Methode), sondern mußte mit einem Gemisch von Aqua dest., Methylbenzoat, Azeton und Glyzerineiweiß erfolgen.

Gefärbt habe ich mit Hämatoxylin nach Delafield-Erythrosin bezw. Azophloxin, mit Eisenhämatoxylin nach Weigert-Azophloxin, ferner mit Pikrokarmin und Toluidinblau. Geschnitten wurde mit 5, 7, 10, 15 und 20 μ.

B. — ZENTRIFUGIERVERSUCHE

1. *Lasius flavus* ♀♀ *Larven.*

Das Material entstammte der unmittelbaren Umgebung von Würzburg (Underdürrbach). Es wurde im März eingesammelt und in Kunstnestern weitergezogen. Die Larven wurden nach etwa 2 Wochen Gefangenschaft zentrifugiert. Untersucht wurde das Stadium am 3. Tag nach dem Einspinnen in den Kokon. Der Kot war im allgemeinen schon ausgetreten. Um die Weiterentwicklung besser beobachten zu können, mußte ich vor dem Zentrifugieren in jedem Falle den Kokon entfernen. Larven, die bereits 24 Stunden nach dem Einspinnen vom Kokon befreit wurden, zeigten noch lebhafte Bewegungen mit dem Vorderende. Eine nochmalige Bildung eines Kokons konnte ich nie beobachten. Auch unterblieb stets das Einspinnen, wenn die Larven einige Zeit daran gehindert d. h. stets in Bewegung gehalten wurden.

Zentrifugiert wurde immer in Abdominallage. Die so behandelten Larven wurden in das Versuchsnest zurückgegeben, und der Eintritt des Puppenstadiums sowie das Schlüpfen der Imagines genau festgestellt. Die ♀♀ wurden reichlich gefüttert, um zu verhindern, daß sie die eigene Brut fressen.

Ergebnisse: Eine, besonders bei den stärker und länger zentrifugierten Larven erwartete Verzögerung der Weiterentwicklung, wie sie Guareschi (1934 *a*) bei den Puppen von Lina populi gefunden hatte, trat *nicht* ein. Innerhalb einer zu erwartenden Variationsbreite verpuppten sich sämtliche Larven, und die Imagines schlüpften ebenfalls in dem normalen Zeitraum. Für jede Versuchsreihe setzte ich mehrere Kontrollversuche (nicht zentrifugierte) an. Jeder Versuch wurde zwei Mal durchgeführt. Die angegebenen Resultate stützen sich auf ein Material von etwa 800 zentrifugierten Larven. Die Temperatur betrug während der von März bis Mai laufenden Behandlungen 21°-22° C. zentrifugiert wurde mit 2 100 U/Min. (Tabelle 1) und 2 500 U/Min. (Tabelle 2) und zwar 1/2, 1, 2, 3, 4, 5 und 10 Minuten lang.

Aus den Ergebnissen geht hervor, daß eine Entwicklungsverzögerung nicht festzustellen ist. Wahrscheinlich ist die Sedimentationswirkung zu geringfügig und vor allem wieder leicht reversibel.

Die geschlüpften Imagines zeigten, rein äußerlich, keine Mißbildungen, es traten in keinem Falle irgendwelche Krüppelformen auf, die auf Grund der — freilich recht unspezifischen — Einwirkung der Zentrifugalkraft hätten erklärt werden können. Fast sämtliche geschlüpften Individuen waren jedoch „Pygmäen" (Mikrergaten), Formen, die rein größenord-

Tabelle 1.

O = nicht zentrifugierte Tiere ; 1/2, 1, 2, 3, 4, 5, 10 = Minuten der Zentrifugierung mit 2 100 U/Min. ; D = Durchschnitt ; die übrigen Zahlen die Anzahl der Tage.

	0	1/2	1	2	3	4	5	10	D
Vom Einspinnen der Larven bis zum Auftreten der ersten Puppen.	8	8	8	7	7	9	8	7	8
Vom Auftreten der ersten bis zur letzten Puppe.....	11	9	9	11	12	15	5	12	11
Vom Einspinnen bis zum Auftreten der ersten Imago	32	30	30	32	32	31	31	32	31

Tabelle 2.

O = nicht zentrifugierte Tiere, 1/2, 1, 2, 3, 4, 5, 10 = Minuten der Zentrifugierung mit 2 500 U/Min. ; D = Durchschnitt ; die übrigen Zahlen die Anzahl der Tage.

	0	1/2	1	2	3	4	5	10	D
Vom Einspinnen der Larven bis zum Auftreten der ersten Puppen.	7	7	7	8	8	7	11	9	8
Vom Auftreten der ersten bis zur letzten Puppe.....	10	8	8	8	7	11	8	13	9
Vom Einspinnen bis zum Auftreten der ersten Imago	31	31	31	31	30	34	33	33	32

nungsmäßig, auffallend weit hinter den eingefangenen ☿☿ standen. Nach Emery (1904) kommen für das Auftreten verschieden großer ☿☿ nur trophogene Faktoren in Betracht, während Forel (1904) sich mit dieser Erklärung „nie befreunden“ konnte. Wheeler (1937) vertritt in seiner letzten Arbeit die Ansicht von Emery mit der Einschränkung, daß nur gewisse Formen, darunter eben die Mikrergaten, ernährungsbedingt auftreten: “In a paper of 1908 and in my ant-book of 1910, sixteen aberrant forms were defined, but four of these, the macrogyne, micrergate, desmergate, and pterergate, should not be included among the anomalies because they are obviously normally recurring variations, or phaenotypes, traceable to deficient or abundant larval feeding.” — Wenn man aber bedenkt, daß die Larven, die nahezu ausgewachsen waren, nur noch etwa

14 Tage im Kunstnest weitergefüttert wurden, dann ihre Nahrungsaufnahme einstellten und anschließend behandelt wurden, so glaube ich kaum, daß *nur* trophogene Faktoren hätten wirksam werden können, zumal die Nahrung ausgesprochen gut und reichlich war (Honigwasser mit fein gehackter Mäuseleber). Die Möglichkeit der Annahme blastogener Faktoren fällt von vornherein weg, denn dann hätten zumindest auch größere ☿☿ auftreten müssen, da das Material aus einem alten Nest stammte ; eine Aufzucht von kleinen ☿☿ stand nicht bevor, wie normal entwickelte ☿☿ zeigten. Trotzdem ist nicht anzunehmen, daß das Auftreten von Mikrergaten auf die ausschließliche Wirkung der Zentrifugalkraft zurückzuführen ist. Vielleicht wirken die neuen allgemeinen Umweltbedingungen (Ortsveränderung, Kunstnest) indirekt stimulierend ein.

2. *Lasius flavus* ☿☿ *Imagines.*

Den Versuchen gingen zunächst Betäubungsexperimente voraus, um ein sicheres Durchführen einer orientierten Zentrifugierung zu gewährleisten. Chloroform und Aether erwiesen sich als wenig geeignet, da die *Dosis tolerata* genau ermittelt werden mußte ; darüber hinaus waren die Wirkungen der Zentrifugalkraft von Betäubungseffekten überlagert, so daß keine sicheren Resultate erhalten werden konnten. Ich zentrifugierte zunächst unorientiert und gab je ein Tier in ein Zentrifugengläschen. Zentrifugiert wurde 10 Minuten lang je 3 600 Umdrehungen.

Ergebnisse: 1/3 der behandelten Tiere war sofort tot, der Rest zeigte, ins Versuchsnest zurückgegeben, schleppende, langsame Bewegungen. Die Extremitäten waren teilweise „gelähmt". Einige der Tiere erholten sich nach einiger Zeit wieder. Brut (Larven und Puppen) wurde vorerst nicht angenommem und ignoriert. Beigefügtes Nestmaterial begannen die Tiere jedoch nach kurzer Zeit lebhaft zu bearbeiten. Nahrung wurde sofort, aber zögernd angenommen. In den folgenden 2 Tagen gingen noch einige Tiere ein, der Rest, etwa die Hälfte, war jedoch annähernd „normal" ; nach 4 bis 6 Tagen änderte sich das Bild nicht mehr. Ein kleiner Unsicherheitsfaktor ließ sich jedoch nicht ausschalten : mit einer Selbsttötung der Tiere durch Verspritzen von Ameisensäure mußte gerechnet werden.

Als brauchbares Betäubungsmittel erwies sich später gasförmiges Kohlendioxyd. Die Betäubung hält zwar nicht lange an, hat aber den Vorteil, daß keine Nebenwirkungen auftreten. — Die Ergebnisse bei orientierter Zentrifugierung wichen von den oben geschilderten etwas ab. Die Anzahl der toten Tiere war sehr gering, sie betrug stets weniger als die Hälfte. Vielleicht spielt die eingenommene Lage bei der unorientierten Zentrifugation eine entscheidende Rolle. Zwischen Kopf- und Abdominallage konnten indessen kaum Unterschiede festgestellt werden.

Da zu den eben geschilderten Versuchen verschieden große ☿☿ herangezogen wurden, drängte sich die Frage auf, extrem polymorphe ☿☿ daraufhin zu untersuchen. — Es wurden Mikrergaten und Makrergaten

ausgesucht und 10 Minuten lang je 3 600 Umdrehungen orientiert zentrifugiert.

Bei den Mikrergaten war ca. 1/6 der behandelten Tiere sofort tot bzw. ging im Verlauf der folgenden zwei Tage ein. Der Rest war zum Teil völlig normal, zum Teil traten Krüppelformen auf, wie sie weiter unten noch beschrieben werden. Bei den Makrergaten war ungefähr ein 1/7 der Tiere tot, der Rest mehr oder weniger beschädigt, nur wenig normale. — Die Ergebnisse beziehen sich sowohl auf Kopflage als auch auf Abdominallage, da hierbei Unterschiede nicht festzustellen waren. Die mehrmals wiederholten Versuche zeigten übereinstimmend, daß ein Unterschied in der Widerstandsfähigkeit der polymorphen ☿☿ nicht zu finden ist.

3. *Lasius flavus* ♀♀ *Puppen.*

Das Material stammte ebenfalls aus der Gegend um Unterdürrbach. Die eingesponnenen Puppen wurden dekokonisiert und in Kopf- und Abdominallage zentrifugiert. Als Ausgangsalter wurde das Stadium, das mit dem Erscheinen der Augenpigmentierung charakterisiert ist, gewählt. Sämtliche zentrifugierten und sogar sämtliche „normalen" Tiere gingen nach einigen Tagen ein. Ich führte diesen Fehlschlag auf die große Empfindlichkeit der Kokon spinnenden Geschlechtstierbrut zurück und ließ für die Wiederholung der Versuche den Kokon bei. Um orientiert zentrifugieren zu können, richtete ich mich nach dem Kotfleck am Kokon, dessen Auftreten zugleich als Ausgangsstadium diente. Die ins Versuchsnest zurückgegebenen behandelten Tiere wurden von den ☿☿ weitergepflegt, während kokonlose Puppen zum größten Teil getötet wurden.



5 mm.

Abb. 1. — Vergleich zwischen einer zentrifugierten (rechts) und einer nicht zentrifugierten Puppe von Lasius flavus.

Ergebnisse: Nach ca. 5 Tagen schlüpften Kontroll- und Versuchstiere. Die stärker und länger zentrifugierten gingen sämtlich ein. Abb. 1 zeigt zur Veranschaulichung die äußeren Unterschiede zwischen einer zentrifugierten (rechts) und einer nicht zentrifugierten (links), „normalen" Puppe. Bei den schwächer zentrifugierten Puppen zeigten die Imagines teilweise Mißbildungen, die nach einiger Zeit zum Tode führten. Diese Mißbildungen wiesen im allgemeinen das gleiche Bild auf : Flügel pupal (hell gefärbt und nicht entfaltet), Gaster auf den Thorax aufgeschoben, Abdomen hell, nicht ausgefärbt und noch in der Puppenhülle steckend, Hinterextremitäten heller als die vorderen und „steif". Die Bewegungen

dieser Tiere waren schleppend, Nahrung wurde in den seltensten Fällen angenommen (Abb. 2).

Die erhaltenen Ergebnisse stelle ich graphisch dar, wobei auf der



Abb. 2. — Vergleich zwischen zwei Lasius ♀. Das rechts Abgebildete wurde auf frühem Puppenstadium zentrifugiert. Vergleiche hierzu Abb. 1.

Ordinate die Sterblichkeit in % und auf der Abszisse die Stärke und Dauer der Zentrifugierung abgetragen ist (*Abb.* 3). Die Resultate

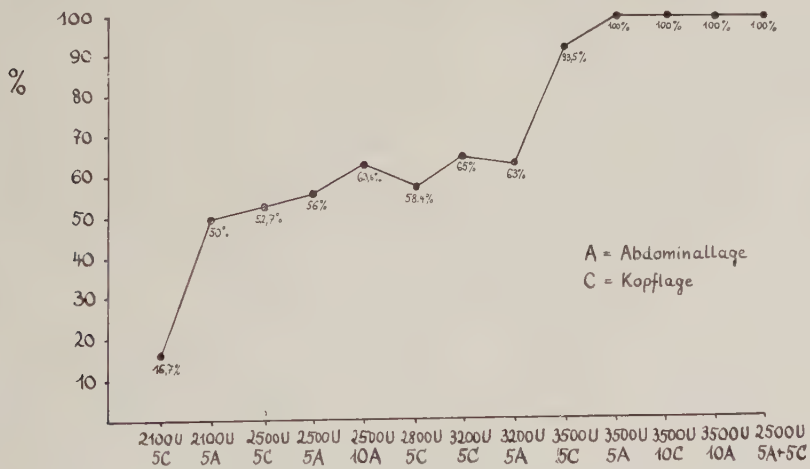


Abb. 3. — Graphische Darstellung der Zentrifugierergebnisse von Lasius ♀♀ Puppen. Die Kurve gibt die Sterblichkeit in % bei entsprechender Zentrifugierung an. — Die Zahlen vor A oder C bedeuten die Dauer der Zentrifugierung in Minuten. Die übrigen Abszissenzahlen die Umdrehungen der Zentrifuge in der Minute.

beziehen sich auf ca. 450 Tiere. Ein großer Unterschied zwischen Kopf- und Abdominallage war nicht festzustellen. Merkwürdig war vor allem die Tatsache, daß, gleich ob in Kopf- oder Abdominallage zentrifugiert wurde,

das Abdomen stets weißlich blieb. Diese Befunde decken sich mit den Ergebnissen von Guareschi (1934 *b*), die dieser bei den Puppen von Lina populi erhielt. Er gibt jedoch nicht an, in welcher Lage er die Puppen zentrifugiert hat. Ueber seine Ergebnisse schreibt er : "... ed in questi casi sempre più nella parte anteriore del corpo che non nell'addome, il che conferma ancora una volta l'esistenza delle duo zone di diversa suscettibilità da me ammessa nella nota precedente." Danach ist also das Abdomen empfindlicher gegenüber der Einwirkung der Zentrifugalkraft als Kopf und Thorax. Dies mag zutreffen, ist jedoch keine Erklärung für das Ausbleiben der Färbung bzw. für das Beibehalten des puppenhaften Aussehens. Vielleicht ist durch die Zentrifugierung der Transport von Verpuppungshormonen gestört worden, die — obwohl noch nicht nachgewiesen — sicher auch bei Formiciden angenommen werden dürfen. Um diesem Fragenkomplex weiter nachzugehen, führte ich Schnürexperimente durch ; deren Ergebnisse bleiben einer späteren Veröffentlichung überlassen.

4. *Tetramorium caespitum* ♀♀ *Puppen.*

Als Material dienten mir ♀♀ Puppen, die aus Unterdürrbach stammten. Es wurden Altpuppen, die fast ausgefärbt waren und ca. 4 Tage vor dem Schlüpfen standen und Jungpuppen, bei denen die Augenpigmentierung noch nicht eingesetzt hatte, verschieden langer und starker Zentrifugierung unterworfen. Kontrollversuche wurden angesetzt ; zentrifugiert wurde in Kopf- und Abdominallage. Da Tetramorium keinen Kokon ausbildet, ist die Altersbestimmung leichter; die Exaktheit der Ergebnisse ließ aber anfangs zu wünschen übrig, da viele behandelte Puppen, die äußerliche Deformationen erlitten hatten, von den ♀♀ erbissen wurden. Ich verminderte daraufhin die Anzahl der ♀♀, bzw. entfernte sie schließlich ganz. Für die Schlüpfzeit wurden wieder welche hinzugegeben. Ich beobachtete keinen Fall einer Tötung mehr, so daß die folgenden Ergebnisse gesichert erscheinen dürften.

Ergebnisse : Nach 4 Tagen, also mit den Kontrolltieren, schlüpfte der größte Teil der zentrifugierten Puppen. Wie bei Lasius zeigte sich, daß die Stärke und Dauer der Zentrifugierung zu den eingegangenen Tieren in einem bestimmten Verhältnis stand, d. h. es ließ sich nach einer Zentrifugierung voraussagen, wieviel Prozent der Tiere wahrscheinlich eingehen würden (*Abb.* 4). Von den geschlüpften, stärker zentrifugierten Tieren zeigten fast alle die schon oben erwähnten Mißbildungen. Nahrung wurde von allen angenommen. Die Bewegungen waren schleppend ; die Hinterextremitäten steif. Das Abdomen blieb nur teilweise hell, pupal. In einem Falle trat ein ♀ auf, das drüsig-geschwollene, mit einer wäßrigen Flüssigkeit gefüllte Vorderflügelspitzen hatte, die am Boden entlang schleiften. Die linke Flügelspitze war stärker angeschwollen als die rechte. Guareschi (1934 *b*) beschreibt bei Käferpuppen ähnliche Befunde : "Elitra sinistra di colore e consistenza dell' adulto, di grandezza e posizione ninfale ;

elitra destra gonfia e ripiena di liquido. Ali piccole, malformate prive delle ripiegature." Als mir später „Normaltiere" die gleichen Mißbildungen zeigten, war es, wenigstens in meinem Falle, erwiesen, daß letztere keine Folgen der Zentrifugierung waren.

Bei den jüngeren Puppen war eine geringfügige Entwicklungsverzögerung und eine geringere Empfindlichkeit gegenüber der Einwirkung der Zentrifugalkraft festzustellen. Die gefundenen Zahlen beziehen sich auf ca. 280 Tiere.

Die *histologische* Untersuchung ergab keine auffälligen Veränderungen der inneren Organe. Lediglich bei Zentrifugierung in Abdominallage trat

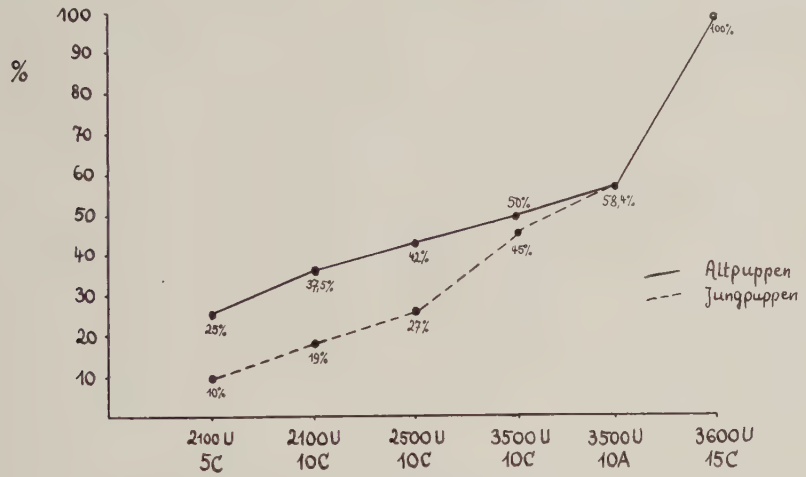


Abb. 4. — Graphische Darstellung der Zentrifugierergebnisse von jüngeren und älteren Tetramorium ♀♀ Puppen. Die Kurven geben die Sterblichkeit in % bei entsprechender Zentrifugierung an. Weitere Erklärungen in Abb. 3.

eine geringfügige dorsale Verlagerung des Mitteldarms ein. Auch bei den anderen untersuchten Ameisenarten konnten keine charakteristischen Abnormitäten festgestellt werden.

5. *Tapinoma erraticum* ☿☿ *Imagines.*

Die hier gewonnenen Ergebnisse gleichen denen von *Lasius flavus* so sehr, daß ich auf eine ausführliche Wiedergabe verzichte. *Tapinoma* erschien jedoch durchschnittlich weniger empfindlich.

6. *Tapinoma erraticum* ♀♀ *Imagines.*

Zentrifugiert wurden ältere ♀♀, die gerade in der Hauptlegezeit standen, 10 und 30 Minuten lang je 3 600 Umdrehungen orientiert und unorientiert. Die Resultate waren überraschend, denn kein Tier zeigte irgendwelche Schäden.

Ergebnisse: In das Versuchsnest zurückgegeben, rannten die ♀♀ umher ; Kontakt mit den ☿☿ wurde sofort aufgenommen, Nahrung nicht verschmäht und nach kürzester Zeit dem Brutgeschäft wieder nachgegangen. Zwecks Prüfung der Eiablage isolierte ♀♀ legten innerhalb der nächsten 20 Stunden nach Zentrifugierung 4—8 Eier ab, die z. T. sofort, z. T. später fixiert wurden, z. T. weiter aufgezogen wurden. Das *histologische* Bild zeigte bei den sofort und später fixierten Eiern gegenüber dem normaler Eier keinerlei Unterschiede. Wahrscheinlich war die durch die Zentrifugierung bewirkte Umschichtung noch zu schwach ; Reith (1933) stellte bei *Lasius niger*-Eiern fest, daß eine gewisse Rückschichtung bald eintrat, wenn die angewendete Zentrifugalkraft gering (unter 30 Minuten) war. Die aus den weiterentwickelten Eiern schlüpfenden Larven und die später auftretenden Imagines zeigten keine Mißbildungen.

Zusammenfassung.

Bei einer gewissen Tourenzahl und Dauer der Zentrifugierung sterben die Objekte ab (vgl. auch Guareschi, 1934 *a*, *b*). Diese Tourenzahl, die ich als die *kritische* bezeichnen möchte, scheint für die einzelnen Arten spezifisch zu sein. So vertragen Tetramorium ♀♀ Puppen im Mittel eine stärkere Zentrifugierung als gleichaltrige Lasius ♀♀ Puppen. Die kritische Tourenzahl beträgt für Tetramorium etwa 3 500 U/15 Min., für Lasius etwa 3 500 U/5 Min. Für Lina scheint sie nach Guareschi bei 3 000 U/10 Min. schon überschritten zu sein. Daß auch bei Eiern Unterschiede in der Widerstandsfähigkeit der einzelnen Arten auftreten, geht aus den Untersuchungen von Reith (1933) hervor. Er stellte fest, daß die Sterblichkeit nach dem Zentrifugieren bei Lasius-Eiern größer war als bei Camponotus-Eiern.

Auf frühem Puppenstadium zentrifugierte Objekte erwiesen sich als empfindlich in dem Sinne, daß die erlittenen Deformationen im Verlaufe der Weiterentwicklung durch die Chitinerhärtung „fixiert" wurden und auf diese Weise Mißbildungen auftraten. Aeltere zentrifugierte Puppen waren gegen solche Zusammenschiebungen widerstandsfähiger. Mit der Sterblichkeit verhielt es sich jedoch fast genau umgekehrt : Jungpuppen sind resistenter als Altpuppen. Larven scheinen von allen Entwicklungsstadien am unempfindlichsten zu sein, soweit man nur niedrige Tourenzahlen berücksichtigt.

Eine durch Zentrifugieren bewirkte Entwicklungsverzögerung trat nur in einigen Fällen ein und dann nur bei solchen Objekten, die auf frühem Puppenstadium behandelt wurden.

Mikrergaten und Makrergaten unterscheiden sich nicht durch verschiedene Widerstandsfähigkeit.

Die Frage, ob ☿☿ Brut oder ♀♂ Brut empfindlicher gegenüber der Einwirkung der Zentrifugalkraft ist, läßt sich nicht exakt beantworten. Meine Ergebnisse tendieren jedoch zu der Annahme, daß Geschlechtstier-

brut nicht so widerstandsfähig ist wie gleichbehandelte Arbeiterinnenbrut.

Aehnlich verhält es sich mit den Unterschieden zwischen Geschlechtstierimagines und Arbeiterinnenimagines, jedoch scheinen hier die Verhältnisse genau umgekehrt zu liegen.

Ein großer Teil der Objekte war gegen Zentrifugation in Kopflage resistenter. Ich möchte jedoch diesen Befund nicht verallgemeinern.

Die histologische Untersuchung ergab in allen Fällen keine charakteristischen Veränderungen der inneren Organe (Sedimentationen), wenn man von geringfügigen Dislokationen des Mesenterons gegen die Dorsalseite hin absieht.

Aus Eiern, die nach der Zentrifugation eines Weibchens von diesem gelegt wurden, entwickelten sich normale Brut und normale Imagines.

Résumé.

La présente étude traite d'expériences de centrifugation pratiquées sur les Fourmis. Il s'agissait de démontrer l'effet de la force centrifuge sur les Fourmis en comparant les résultats obtenus à ceux de Guareschi.

Les insectes utilisés dépérissent dès qu'on atteint un certain nombre de tours et une certaine durée de centrifugation (voir aussi Guareschi, 1934, *a*, *b*). Ce nombre de tours, que j'appellerai le *nombre critique*, semble être spécifique. Ainsi des nymphes ♀♀ de *Tetramorium* supportaient en moyenne une centrifugation plus forte que des nymphes ♀♀ de *Lasius* du même âge. Pour *Tetramorium*, le nombre critique de révolutions s'élève à environ 3 500 par minute pendant 15 minutes, alors qu'il est d'environ 3 000 par minute pendant 5 minutes pour *Lasius*. D'après Guareschi, pour *Lina*, le nombre critique semble déjà être franchi à 3 000 révolutions par minute pendant 10 minutes. En ce qui concerne les œufs, il ressort des recherches de Reith (1933) qu'il y a aussi des différences quant à la capacité de résistance des diverses espèces. Reith a constaté que la mortalité après centrifugation était plus élevée avec les œufs de *Lasius* qu'avec les œufs de *Camponotus*.

Des insectes centrifugés au premier stade nymphal se montrent sensibles en ce sens que les déformations subies pendant la centrifugation sont fixées par la chitinisation au cours du développement ultérieur, et qu'ainsi on peut obtenir des Fourmis difformes. Des nymphes plus âgées sont plus résistantes à de pareilles déformations. Cependant, la mortalité varie presque en raison inverse, les jeunes nymphes étant plus résistantes que les vieilles. Parmi tous les stades de développement, les larves semblent être les moins rapidement sensibles.

La centrifugation ne produit de retard dans le développement que chez les individus traités au début du stade nymphal.

Quant à la capacité de résistance des micrergates et celle des macrergates, elles ne diffèrent pas.

On ne saurait dire de façon précise si c'est le couvain ♀♀ ou le couvain ♂♂

qui est le plus sensible à l'effet de la force centrifuge. Cependant, les résultats de mes recherches permettent de supposer que le couvain sexué n'est pas aussi résistant que le couvain ouvrier traité de la même manière.

Une différence de même ordre se marque entre imagos sexués et ouvriers, mais au bénéfice des premiers.

Une grande partie des objets étaient plus résistants à la centrifugation si leurs têtes se trouvaient détournées du centre de rotation. Cependant, je ne voudrais pas généraliser ce résultat.

Dans tous les cas vérifiés, l'examen histologique ne montrait aucun changement des organes internes, c'est-à-dire des sédimentations, à part des dislocations sans importance du mésentéron vers le côté dorsal.

Des œufs qui avaient été pondus par une femelle après qu'elle avait été centrifugée donnaient un couvain normal et des imagos normaux.

Summary.

The above research work deals with experiments on the effects of centrifugal force on ants. Its object was to ascertain how ants react to the action of centrifugal force. The results obtained were compared with those obtained by Guareschi.

When the objects used in the experiments were exposed to centrifugation, they died at a certain rate of revolutions per minute applied during a certain space of time (cf. Guareschi, 1934, *a*, *b*). The number of revolutions which I should call the *critical* one, seems to be specific for the various species. Thus ♀♀ pupae of *Tetramorium* will on an average endure a higher rate of revolutions than ♀♀ pupae of *Lasius* of the same age. The critical number of revolutions for *Tetramorium* approximately amounts to 3,500 r.p.m. during 15 min., whereas for *Lasius* it is approximately 3,500 r.p.m. during 5 min. According to Guareschi, the critical number for *Lina* seems to be exceeded at a lower rate of 3,000 r.p.m. during 10 min. The result of Reith's investigations (1933) was that with eggs there are also variations in the power of resistance to centrifugation according to the species. He stated that mortality after centrifugation was higher with eggs of *Lasius* than with eggs of *Camponotus*.

Objects that were centrifuged at an early pupal stage proved sensitive to centrifugation as was shown by deformities resulting from deformations suffered during exposure and fixed by the hardening of chitin in the course of further development. Older pupae showed more power of resistance to such deformations. As to mortality, however, it can be said that almost the contrary was true: young pupae are more resistant than old ones. Among all the stages of development, larvae seem to be least sensitive as far as only low numbers of revolutions are taken into account.

A certain delay in development caused by centrifugation did not occur

but in a few cases, and if so, occurred only in such objects as had been treated at an early pupal stage.

Microergates and macrergates do not differ in their power of resistance.

The question whether ♀♀ brood or ♂♂ brood is more sensitive to the effects of centrifugal force cannot exactly be answered. Yet the results of my investigations allow to suppose reproductive brood to be less resistant to centrifugation than worker brood exposed to the same proceedings.

It is similar as to the differences between reproductive imagos and worker imagos, yet in that case just the contrary seems to prevail.

When the heads of the objects found themselves in opposition to the rotational centre, a considerable part of them proved more resistant in such a position. Yet I refrain from generalizing that result.

In all the cases histological investigation did not show any typical changes in the internal organs, i.e. sedimentations, not reckoning insignificant dislocations of the mesenteron towards the dorsal side.

From eggs laid by a female after its exposure to centrifugation resulted normal brood and normal adults.

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WINTER BROOD AND POLLEN IN HONEYBEE COLONIES

by

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INTRODUCTION

Nolan (1925) has provided a good record of the quantities of brood in honeybee colonies during the summer months, but the position over winter, though fundamentally no less interesting, has been far less certainly investigated. This has been the result of the very strong tradition that bees should be left strictly alone during the winter—a tradition which, with discretion and common sense, may be broken much more freely than is usually imagined. Wedmore (1947) discussing temperature relationships in the colony, and basing his ideas apparently in considerable measure on logical deduction, and without bringing forward the necessary experimental evidence on the winter cluster, presents views which nevertheless seem in some essential details to coincide with the present observations. He says that after an autumnal period of quiescence during which the bees are avoiding the formation of a tight cluster, the onset of cold weather compels them to cluster more closely, and that this forces the temperature up at the centre of the cluster. He considers that, given adequate supplies of pollen, breeding may commence before the end of December, or as soon as the period of tight clustering sets in, in accomodation to the prevailing cold weather. Butler (1954) gives a somewhat similar impression when he says "between the middle of November and February honeybee colonies in Britain contain very little, if any, brood", and "sometime after Christmas, usually early in February, brood rearing begins again". Farrar (1949) while giving evidence of brood soon after January 1 in a colony, presents the viewpoint that winter brood rearing can be brought about by added supplies of pollen, and that it is both normal and beneficial. From less informed sources, wider divergencies of opinion on the date of commencement of brood rearing could be quoted; and it seems desirable therefore to bring forward experimental evidence extensive enough to give an adequate picture of the real position.

Several more or less sporadic observations of the state of the brood nest in winter have been made, often after the colonies in question have met with some disaster. In addition, Farrar (1949) gives details of the winter cluster based on several colonies killed with cyanide. No worker, however, appears hitherto to have made systematic measurements of bees, brood and pollen on large numbers of living colonies in every winter month, including a considerable number of consecutive years, and with the assurance that the bees had been free from disease and had not been subject to disastrous conditions, or previous accidental mis-management (leading for example to queenlessness in late summer, which may radically alter the quantity of pollen present at the autumn examination; or starvation, which may modify the quantity of brood).

METHOD

During the winters between 1945 and 1954 a number of honeybee colonies were wintered in the College research apiary. All were microscopically tested as a matter of routine in autumn and again in spring for Nosema, acarine and amoeba diseases, and the colonies chosen for this series of observations were all healthy at each of these examinations. All were wintered without packing, mostly in Modified National hives, and all were queenright colonies which had, except for some occasional brief intervals, been run in a queenright condition during the previous summer; with marked queens not exceeding two years old.

On selected mild days in the months September to March, inclusive, quantities of total brood (including eggs) and quantities of pollen stored in the combs were determined in square inches, by means of a specially constructed wire grid, 13.50 ×7.41 inches in size, shaped approximately to the forms of developing brood areas, but nevertheless divided into exact areas of 1 square inch, with main divisions (marked in distinctive colours) every 10 square inches.

Numbers of bees were also determined in the colonies either by the technique of comparing quantities of bees on the combs with calibrated photographs (JEFFREE, 1951), or by a technique of direct weighing (JEFFREE, 1955).

Honey was extracted from other combs similar to those left as winter stores with the above colonies, and quantities of pollen in the previously capped cells were measured.

RESULTS

The results of 367 examinations made during September to March inclusive over 9 years (September 1945, to December, 1953) showed the following average areas of pollen and brood per colony.

TABLE 1. — *Brood and Pollen found on 367 examinations from September to March.*

	POLLEN SQ. INS. (average).	BROOD SQ. INS. (average).	NO. OF COLONIES.	% OF COLS. WITH BROOD.
September	29	76	45	78
October	17	2	106	14
November	23	2	114	25
December	26	10	31	58
January	22	14	18	50
February	32	48	10	100
March	14	50	43	91
Mean	23	29	52	59

The number of bees in these colonies averaged 13,185 in September and 10,131 in February.

Honey from other colonies was extracted from more than 200 combs similar to the combs of winter stores left with the above colonies, and the total quantity of pollen in the previously capped cells (as distinct from that in uncapped cells reported above) amounted to 15 square inches for 766 lbs. of honey extracted.

Most of the colonies represented in Table 1 were examined only twice during the seven months. Seven of these colonies were, however, each examined four or more times, and Table 2 gives the dates of examinations and shows whether brood was present (+) or absent (—) on each occasion.

TABLE 2. — *Brood present or absent on individual examinations of 7 colonies.*

Colony A	15.11.45	6.1.46	5.2.46	6.3.46	
	+	+	+	+	
Colony B	6.9.45	16.9.45	26.9.45	6.10.45	15.11.45
	+	+	+	+	+
	6.1.46	5.2.46	6.3.46	27.3.46	
	+	+	+	+	
Colony C.....	7.9.45	16.9.45	6.10.45	15.11.45	6.1.46
	+	+	—	—	—
	5.2.46	6.3.46	27.3.46		
	+	+	+		
Colony D	17.9.46	18.10.46	27.11.46	15.1.47	25.3.47
	+	—	+	—	+
Colony E	17.9.46	18.10.46	6.11.46	4.12.46	16.1.47
	—	+	+	—	—
	25.3.47				
	—				
Colony F	17.9.46	17.10.46	27.11.46	19.12.46	17.1.47
	—	—	+	+	+
	25.3.47				
	+				
Colony G	25.9.47	21.11.47	24.12.47	10.2.48	12.3.48
	+	—	+	+	+

DISCUSSION

The figures in Table 1 show that at Aberdeen the quantity of brood in the months when bees are wintering drops to a minimum in October and November. In October only one in seven of the colonies examined had brood. In November the ratio had risen to one in four, and in December and January brood was present at half of the examinations. In February and March, twelve colonies out of every 13 had some brood. Table 2 suggests that some colonies (as Colony B) may have had brood throughout the winter, others (as Colony D) had some intermittently, while others (Colonies C, G and F) may have had just one fairly long broodless interval, persisting in breeding once they had started again.

The actual quantities of brood present were almost always very small compared with summer levels (the latter often amounting to 1,000 sq, ins.), and the frequency of appearance tended to increase from October onwards. With such variability of performance, however, it is hardly surprising that authors have given rather variable views on the time when bees start to breed. These results coincide fairly closely with Wedmore's idea of a period of quiescence followed by brood-rearing as soon as colder conditions set in; but nevertheless attempts in this laboratory to correlate the amount of brood in individual winter months with temperature fluctuations have not so far been successful.

It will be noticed that these quite strong, healthy colonies had on an average only 23 sq. inches of pollen in the combs. This quantity is equivalent to 3 oz. of pollen, and is much less than Farrar (1934, 1936) considers desirable, but, under Aberdeen conditions at least, it would seem closely to represent the quantity naturally present in colonies that have not been specially manipulated in respect of pollen, and that have not been queenless during late summer. The measurement of the quantity of pollen stored in capped cells indicates that the approximately 25 lb. of honey uncapped and consumed by the bees of a colony during the 7 months discussed above will be associated with only about 0.5 sq. ins. of pollen in capped cells, an amount which is negligible in comparison with the average of 23 sq. ins. left uncapped.

Unless there are wide differences in different climatic zones, it would, therefore, be reasonable to conclude that in their natural economy honeybees winter practically without any major amount of pollen (or protein) but consume only honey, a fairly pure mixture of carbohydrates: and since they would apparently have come to do this in the face of natural selection, it is perhaps a fact worth thinking about. It would seem not impossible that just as flowers have been modified by natural selection into forms which make their pollen conveniently available to bees, so the nectar of flowers may have become modified into a very pure form of carbohydrate (with in general very low levels of protein) partly because absence of protein has given the highest survival of overwintering honeybee colonies, able to continue the pollination of the flowers of succeeding seasons. It must be admitted on the other hand, however, that the low protein in nectars could also be a question of providing an ideal mixture for safe storage over winter without fermentation or other deterioration, which again could have been achieved by natural selection.

The nectar of *Calluna vulgaris* (L.) Hull is, among the major sources of nectar utilised by the honeybee in Eurasia, the one well recognised exception to the above rule of low protein content, for ling heather honey often contains 2 to 3% of colloid (Mitchell, Donald and Kelso, 1954); but experience of conditions in Scotland would suggest that it is rather unlikely that honeybees in any case ever survived long in the wild state in the latitudes and altitudes of the main ling heather areas. The extension of such a form of reasoning to the nectars of flowers of the American

continent and the Southern hemisphere, where the natural pollinating insects were different, but where there are a few nectars containing protein, would seem to lie outside the scope of this paper.

My thanks are due to Miss M. D. Allen, who made some of the above measurements in 1953.

Summary.

In 367 examinations of healthy honeybee colonies during each of the months September to March inclusive, conducted over 7 years, the quantities of brood present and the quantities of pollen in the combs were determined. The brood minimum occurred in October, when brood was present in only 14% of colonies, while throughout the period of wintering the quantity of pollen per colony averaged only 3 oz. In colonies which had been queenright, quantities of pollen stored in capped cells were negligible in comparison with quantities in open cells. It is suggested that bees may have come to winter practically without protein as a result of natural selection.

Zusammenfassung.

In 367 Untersuchungen gesunder Bienenvölker während der Monate September bis Ende März über eine Periode von 7 Jahren wurde die Menge anwesender Brut und Pollens in den Waben festgestellt. Die Brutmenge war am niedrigsten im Oktober mit nur 14 % aller Völker, während der Durchschnitt der Pollenmenge per Volk während der Winterungszeit nur 85 gr betrug. In Stämmen mit einer Königin war die Menge des in Waben verkapselten Pollens minimal im Vergleich zu der in unverkapselten Zellen. Es wurde vorgeschlagen, daß Bienen als Resultat natürlicher Auslese fast ohne Eiweiß überwintern.

Résumé.

On a déterminé les quantités de couvain et de pollen dans les rayons de 367 colonies saines examinées de septembre à mars durant sept ans. Quand le couvain était présent dans 14 p. 100 des colonies avec un minimum en octobre, la quantité de pollen par colonie pendant l'hivernage avoisinait 85 grammes en moyenne. Dans les colonies possédant une reine, la quantité de pollen accumulée en alvéoles fermées était négligeable par rapport à celle accumulée en alvéoles ouvertes. L'auteur suggère que la sélection naturelle peut expliquer le fait que les abeilles puissent passer l'hiver pratiquement sans protéines.

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CONTRIBUIÇÃO PARA O CONHECIMENTO DA BIONOMIA DOS MELIPONINI

5. DIVISÃO DE TRABALHO ENTRE AS OPERARIAS DE *MELIPONA QUADRIFASCIATA QUADRIFASCIATA* LEP

By

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INTRODUÇÃO

É sabido que os *Meliponini* possuem divisão de trabalho entre as fêmeas, conforme sejam rainhas ou operárias. A principal finalidade do presente trabalho é dar um relato dos nossos estudos sôbre a divisão de trabalho entre as operárias dos *Meliponini*, de acôrdo com suas idades.

MATERIAL

Usamos para estas observações uma colmeia de *Melipona quadrifasciata quadrifasciata* Lep. (Nº 37), descendente de uma colonia provinda de Pariquera Assú (São Paulo), e aquí recebida a 18/5/48, por especial gentileza do Dr. Paulo Nogueira Neto, a quem somos gratos. Essa colmeia sofreu 3 divisões : a la. em junho de 1948, a 2 a. em junho de 1950 e a 3 a. em maio de 1953. Algumas das colmeias descendentes demonstraram, pela segregação no comprimento das bandas amarelas dos tergitos abdominais, que suas rainhas se acasalaram com machos de *Melipona quadrifasciata anthidioides* Lep. A rainha da nossa colmeia foi fecundada a 15/5/53.

MÉTODOS

Marcamos 13 abelhas nascidas durante a noite até ás 9 horas da manhã do dia 1/7/53, com os seguintes discos : verde : 0,97, 98 ; vermelho : 0,97, 98 ; amarelo : 0,97, 98 ; prata : 0,97, 98 e branco : 0. Das abelhas marcadas foram aceitas sómente 8, a saber : verde : 97 e 98 ; amarelo : 98 ; vermelho : 0,97 e 98 ; prata : 0 e 98.

Essas operárias foram observadas por diversas horas diárias, geralmente numa média de 4 horas em cada dia ; No começo, a observação foi feita com menos tempo, durante o qual repetiram os mesmos afazeres ou, então, descansavam muito, Com mais tempo no final ou quando se percebia alguma mudança importante na vida delas. A última abelha morreu no dia 18/8/1953. A pigmentação dos pêlos e quitina das abelhas desta espécie varia muito, conforme aumentam em idade : portanto, foi facil corroborar e completar os dados obtidos por essas oito abelhas, observando as de igual pigmentação. Uma tabela de referências entre pigmentação e idade será dada em um outro trabalho.

SEQUENCIA DA DIVISÃO DE TRABALHO

1º dia. — Nas primeiras 3 a 4 horas (às vêzes um pouco mais) de vida, as operárias executam a sua limpeza corporal, extraindo restos da última exúvia, limpando seus pêlos, etc. Nesta ação, elas procedem muito mais vigorosamente que as operárias de *Apis mellifera* L. Logo que emergem, procuram alimentar-se, solicitando alimento às abelhas mais idosas (com mais de 9 dias).

1º ao 5º dia. — Após terminarem a "toilette", as operárias gastam a maior parte do seu tempo na incubação, na raspagem da cêra dos alvéolos, no trabalho da cêra, sobretudo, na construção de pilastras que firmam um favo de alvéolos a outro, ou, ainda, um favo a lamelas. Presenciamos, ao 5º dia, uma abelha procedendo à limpeza dos tergitos abdominais das placas de cêra branca, colocando-as, a seguir, diretamente sôbre uma protuberância de uma lamela. Nos últimos dias, vimos abelhas servirem-se de polem dirétamente dos potes, nos quais demoravam de 30 segundos a 7 minutos.

6º ao 8º dia. — Ainda, lidam com cêra, quase exclusivamente no lugar da cria, porém, ocasionalmente, vimo-las trabalhando na construção de um pote. Trabalham bastante na deposição ou remoção de cêra das lamelas. Destroem casulos, removem a cêra de seus interstícios e, esporàdicamente, fazem a côrte à rainha.

No tocante a esta última particularidade, não existe um grupo fixo de operarias incumbido de fazer a côrte a rainha, de modo que, se ela estiver passando, recebe a côrte das mais próximas e, no caso de permanecer parada, então as operárias se revesam contínuamente nesse mistér.

9º ao 11º dia. — Ainda incubam, raspam a cêra e lidam com ela. Pela primeira vez, vimos algumas das abelhas marcadas construindo células ou terminando células recém-operculadas. Uma abelha foi vista fazendo a operculação de uma célula onde a rainha terminara de pôr um ôvo. A maior parte do alimento das abelhas, até o 9º dia lhes é dada por abelhas mais idosas. Entrementes, abelhas contando com 10 dias, ou mais, de idade, foram vistas alimentando as mais jovens, inclusive as recém-emergidas. Fazem a côrte e dão alimento à rainha.

Abelhas de 10 dias foram vistas fazendo limpeza na região da cria. Outra abelha foi vista indo até um montículo de lixo para defecar.

Ao 11º dia colocamos polem de *Apis mellifera* L. no chão da colmeia, fora da zona da cria. Esse polem foi ajuntado e colocado nos montinhos de lixo por abelhas mais idosas que as marcadas (aliás, as poucas marcadas que entraram em contacto com êsse polem alimentaram-se dêle).

12º ao 21º dia. — Ainda incubam, porém menos, só mesmo nas horas mais frias, à noite e até às 10 da manhã mais ou menos. Trabalham, também, com cêra (construindo alvéolos, potes, invólucros, etc.), porém menos que no decêndio anterior ; não as vimos mais segregando cêra. Começam a trabalhar bem mais fora do local da cria. Auxiliam abelhas a emergirem, rompendo o casulo. As operações de limpeza tomam bastante intensidade na região da cria, ao redor do 16º dia, e conforme progridem em idade essa limpeza é estendida ao resto da colmeia, o que acontece ao redor do 20º dia de idade. No 21º dia, vimos diversas operárias levando lixo dos vários montículos para aquêles próximos do lugar das campeiras ; também, ao 21º dia, vimos operárias tirando fundos de alvéolos vasios, operação que não realizavam antes. A operação mais importante que executaram nêste decêndio foi o aprovisionamento dos alvéolos de cria. Essa operação foi realizada, pela primeira vez, ao 13º dia, porém tem seu máximo de intensidade aos 15º, 16º e 17º dia, diminuindo, em seguida, paulatinamente. São as abelhas desta idade que mais alimentam as rainhas.

22º ao 26º dia. — Não constroem mais alvéolos, não alimentam mais a cria; ocasionalmente ainda alimentam a rainha. A limpeza é bem intensa, generalizada a tôda a colmeia. Ainda incubam, porém menos que no decêndio anterior. Ainda raspam e lidam com cêra (menos ainda). Ao 23º dia, pela primeira vez, entraram em contacto com as campeiras, porém eram contactos muito curtos, afastando-se após 10 ou 15 segundos. Ao 24º dia, foi derramado um pouco de mel no assoalho da colmeia, porém, apezar de tôdas terem tido oportunidade, nem uma siquer sugou-o. Uma operária, usou cerúmen para lacrar o vidro da colmeia.

27º ao 30º dia. — Ainda lidam um pouco com cêra, em tôda a colmeia ; incubam se necessário, limpam muito, mudam lixo de um montículo para outro. Vão diversas vêzes ao lugar das campeiras, porém não chegam a trocar sinais de antena. Lidam com cerúmen, lacrando as frestas da colmeia. Ao 27º dia, colocamos (às 15 horas) mel, diluido a 50 %, dentro de uns potes abertos e no assoalho. No início, as abelhas marcadas sugavam por um a dois segundos e afastavam-se, porém, 12 minutos após termos colocado êsse mel, duas abelhas marcadas (O prata e 97 vermelha) iniciaram sua succão e o colocavam diretamente nos potes. Mais 5 minutos e a 97 verde, 98 amarela, O prata e 98 prata também começaram a sugar o mel. Ainda no 27º dia, a abelha 98 amarela recebeu mel de uma campeira e trabalhou como receptora por 10 minutos.

Ao 28º dia, vimos que, pela manhã até cêrca de 10 horas, tôdas estavam incumbando, ou limpando, ou lidando com cêra no lugar da cria, ou auxiliando outras a sairem dos casulos, portanto tôdas em atividades na

região de cria. Entre 10 horas e 10 horas e 15 minutos, começaram a trabalhar fora do lugar da cria (construção de potes, limpeza, recebimento ocasional de mel). Ao 28º dia, 4 abelhas trabalharam à tarde, contínuamente como receptoras de nectar, tendo a 97 vermelha e 0 vermelha sido receptoras dentro do tubo de saida. Ao 29º dia, tôdas já eram receptoras. Um fato importante ocorrido neste dia foi o da abelha 98 vermelha passar boa parte da tarde deshidratando nectar. Ao 30º dia, além das atividades dos 3 dias anteriores, vimos uma abelha (98 amarela) tirando cerúmen da pata de uma campeira e em seguida utilizá-lo para lacrar frestas.

31º ao 33º dia. — Incubam pouco e pouco lidam com cêra (mais durante à noite). Muito ativas nas operações de limpeza e de lacragem com cerúmen. Têm já mais estabilidade na função de receptoras de nectar, 4 delas tendo passado a maior parte da tarde nessa função, e as outras despendido boa parte do tempo nesse trabalho. Conforme as necessidades, algumas trabalharam como deshidratadoras de nectar.

Ao 31º dia, às 17 horas, pela primeira vez, uma operária (98 vermelha) saiu da colmeia, levando um fundo de alvéolo e permaneceu fora cêrca de 3 a 4 segundos.

Ao 32º dia, mas 4 operárias iniciaram-se no vôo fora da colmeia, tôdas na operação de levar o lixo para o exterior da colmeia. É interessante notar que a operária 0 vermelha, ao entrar, errou a porta e penetrou em o nosso laboratório. Neste período, nunca observamos as operárias marcadas na região da cria. Por poucas vêzes, algumas das operárias serviram como guardas. Durante todo o período de observação só 4 serviram de guardas e, mesmo assim, revesando-se em poucos minutos ; por outro lado, nem tôdas serviram como deshidratadoras de nectar.

Ao 33º dia, mesmo à noite, só uma ou outra operária marcada incuba, e, bem cêdo, já se entregam ás operações de levar lixo para fora (agora executado por tôdas as operárias), de recepção, e de deshidratação.

34º ao 37º dia. — Nêste intervalo, as operárias passam por um período de transição da vida de donas de casa para a vida de trabalhos de campo (campeiras). Ao 34º dia, uma operária (98 verde) saiu para coletar xarope de mel a 50 %, colocado a 40 cm da colmeia experimental, tendo trabalhado nesse afã desde às 14 horas (aproximadamente) até às 17 horas e 50 minutos. Nos dias seguintes, essa mesma abelha, no período da manhã até às 13,30 horas, aproximadamente, trabalhava como receptora ou guarda e à tarde coletando xarope.

Neste período, de um modo geral, ocupam-se pela manhã com limpeza, lacragem, raramente incubação ; após às 10 horas, como receptoras, e, à tarde como receptoras, guardas e deshidratadoras. Uma das funções das receptoras é dar alimento às campeiras, mesmo às que trazem nectar.

Ao 36º dia. — Verificamos que, à noite (21 horas), uma só das marcadas estava incubando, parmanecendo as demais escondidas, dentro de potes, sob lamelas de cêra, etc.

Ao 37º dia. — Ainda fazem limpeza. Mais duas operárias saem para o campo, nêste dia, tôdas no período da tarde, regressando com nectar. As

que permaneceram nos trabalhos caseiros transportaram lixo ou eram receptoras.

38º ao 42º dia. — Após o 39º dia, nenhuma abelha foi vista incubando. Ao 38º dia, tôdas foram receptoras no período da manhã, exceto a 98 prata, que se tornou campeira logo às primeiras horas do dia, tendo regressado à colmeia, às 8 horas e 23 minutos, com carregamento de polem. A tarde foram campeiras, trabalhando com nectar, exceto a 98 prata que voltou a ser receptora.

Ao 39º dia, tôdas foram receptoras pela manhã e das 13 horas em diante campeiras, porém, sómente a 97 vermelha o foi constantemente, tendo as outras interrompido frequentemente esta atividade.

Do 40º ao 42º dia, tôdas foram campeiras, todavia, no período da manhã, até aproximadamente às 12 horas do dia 41º, e 9,30 horas do 42º dia, ainda trabalhavam firmes como receptoras.

43º ao 49º dia. — Nas primeiras horas do dia (até 9 horas) ficam aguardando, excitadas, o momento apropriado da partida, e são sempre das primeiras a sair, trabalhando firmes durante todo o dia nêsse serviço. A hora do encerramento do trabalho nêste período foi muito restrito, pois variou entre 17,50 e 18,00 horas.

DISCUSSÃO

Comparando a divisão de trabalho encontrado na *Melipona quadrifasciata quadrifasciata* Lep, com os descritos para *Apis mellifera* L. (Rosch, 1925, 1927, 1930 ; Lindauer, 1953) e para *Bombus agrorum* Fabricius (Brian, 1952), verificamos que, neste respeito, as Meliponas estão muito mais próximas à *Apis mellifera* L. Há, entretanto, duas diferenças fundamentais.

1. A alimentação das larvas em *Apis mellifera* L. dá-se no 1º período de vida, isto é, entre o 3º e 13º dias de vida, e a secreção de cêra dá-se no 2º período de sua vida, atingindo o auge entre os 12º e 18º dias de vida (apesar de, segundo Lindauer, 1953, ambas as funções serem executadas, concomitantemente, diferindo na frequência).

Para a *Melipona quadrifasciata quadrifasciata* Lep. essa ordem acha-se invertida, sendo que os trabalhos com cêra se processam do 1º ao 13º dias com mais intensidade (estendendo-se até o 36º dia se considerarmos as lidas ocasionais também), e a provisão dos alvéolos com alimento do 13º ao 21º dias (com mais intensidade aos 15º, 16º e 17º dias).

2. As operárias de *Apis*, no 2º período (cêra), já saem da colmeia para vôos ocasionais ou como "lixeiras". Para *Melipona quadrifasciata quadrifasciata* Lep. há um período certo, do 27º ao 30º dias, em que as operárias fazem suas primeiras excursões, trabalhando na remoção de lixo.

O tipo de trabalho dos Meliponini e Apini, se tomarmos por base o que sucede às *Apis mellifera* L. e *Melipona quadrifasciata* Lep., pertence a um grupo mais evoluido que o dos *Bombini* (de acôrdo com a observação

em *Bombus agrorum* Fabricius), pois, além de existir uma divisão de trabalho de acôrdo com o alimento recebido (operária e rainha), há também uma divisão muito mais complexa, devido a idade do indivíduo e às necessidades da colmeia.

ABSTRACT

1) Eight newly emerged workers of *Melipona quadrifasciata quadrifasciata* Lep. were marked with different numbers and colors, put back in the observation hive and observed every day for an average of 4 non-continuous hours a day until all died (July 1 to August 18, 1953). Pigmentation varies strikingly in workers of this species according to age: therefore, observations of other individuals corroborated and completed the findings based on the eight marked workers.

2) Their activities can be summarized as follows:

a) *1st to the 11th day.* First four hours: "toilette". Incubation. Production and manipulation of wax in the brood-nest area in the begining and, later on, in the whole colony. Cleaning in the brood-nest area; destruction of used cocoons. After the 9th day, construction of cells for the brood, feeding of younger bees and, occasionally, feeding and courting of queen.

b) *12th to 21st day.* Construction of brood cells, filling them with food, and sealing them. Manipulation of wax in the whole hive. Cleaning, each day farther from the brood nest area, on the 20th day generalized in the whole hive. Incubation when cold.

c) *22nd to 26th day.* Manipulation of wax but no construction or provisioning of cells. Occasionally, feeding of queen and young workers. Intense cleaning. (They sealed cracks with cerumen but did not suck honey pured into the hive). Incubation when cold.

d) *27th to 35th day.* Manipulation of wax. Incubation when cold. Intense cleaning. Manipulation of cerumen. Nectar receiving. (Honey poured on the floor on the 27th day was sucked by all marked bees. On the 27th the first marked bee was seen as a nectar receiver, on the 28th 4 more, and on the 29th all of them. On the 29th one was observed being a dehydrator of nectar). Flying. (On the 31st day one flew out taking out the bottom of a cocoon, on the 32nd 4 more, and on the 33rd all flew. Some served as guards). Beginning of field activities. (From the 34th to the 37th day they passed into a period of change from housekeepers to field bees. On the 34th the first bee left the hive to collect nectar).

e) *36th to 49th day.* Cleaning, carrying materials to outside (37th day). Field activities. (Three other workers became field bees on the 37th; on the 38th all of them. No correlation was observed between the first bees that changed to higher age jobs and the first to become field bees. Usually they collected pollen from 8:30 a.m. to 12:30 p.m. and nectar from 11:00 a.m. to 6:00 p.m. The last time a marked bee was seen

incubating was on the 36th, the last time receiving nectar was on the 42nd, the last time manipulating wax was on the 36th).

3) Comparing the division of labour found in *Apis mellifera* L. and *Bombus agrorum* (Fab.), the authors conclude that *Melipona* is most similar to *Apis*, with two major differences: a) the wax secretion period is more scattered in *Melipona*; the period of greatest intensity is prior to the period of filling the cells with food, while in *Apis* the period of feeding larvae is prior to wax production; b) workers of *Apis* leave the colony, either for working or for occasional flights, when much younger than *Melipona* workers.

Zusammenfassung.

1) Es wurden acht eben geschlüpfte Arbeiterinnen von *Melipona quadrifasciata* Lep. durch verschiedene Farben- und Nummerngebung markiert und dann in das Beobachtungsgehäuse zurückgegeben. Anschließend wurden sie täglich in Zeitintervallen von durchschnittlich zusammen 4 Stunden beobachtet bis sie eingingen (1. Juli bis 18. August 1953). Die Pigmentation der Arbeiterinnen dieser Art variiert sehr je nach Alter. Daher wurden zur Ergänzung der an jenen 8 Arbeiterinnen gefundenen Resultate noch weitere Individuen zur Beobachtung herangezogen.

2) Die charakteristischen Arbeitsverrichtungen können folgendermaßen zusammengefaßt werden :

a) *Vom 1. bis zum 12. Tag:* In den ersten vier Stunden : „Toilette"-Inkubation. Beginn der Wachsproduktion und Verarbeitung im für die Brut reservierten Teil, später im ganzen Nest. Reinigungsarbeiten im Brutnest ; Vernichtung alter Kokone (Puppenhäuschen). Nach dem neunten Tag Brutzellenbau, Fütterung jüngerer Bienen und gelegentlich auch Fütterung und Aufwartung der Königin.

b) *Vom 12. bis 21. Tag:* Brutzellenbau unter Eingeben von Nahrung und Bedekkeln derselben. Wachsverarbeitung im ganzen Stock. Reinigungsarbeiten, jedoch täglich mit zunehmendem Abstand vom Brutnest, später (vom 20. Tag an) allgemein im ganzen Stock. Inkubation bei Kälte.

c) *Vom 22. bis 26. Tag:* Wachsarbeiten, jedoch ohne Bau oder Versorgung von Zellen. Gelegentlich Fütterung der Königin und junger Arbeiterinnen. Intensive Reinigungsarbeiten. (Es wurden Spalten verkittet, aber kein reiner Honig ins Nest gegeben.) Inkubation bei Kälte.

d) *Vom 27. bis 35. Tag:* Wachsarbeiten. Inkubation bei Kälte. Intensive Reinigungsarbeiten. Kittarbeiten. Nektarannahme (Honig, der am 27. Tag auf der „Tenne" (floor) gereinigt worden war, wurde von allen markierten Bienen aufgesogen. Am 27. Tag wurde die erste gezeichnete Biene bei Nektaraufnahme beobachtet, am 28. dagegen vier und am 29. sämtliche. Am 29. Tag konnte ein Individuum bei der Nektarentwässerung beobachtet werden. Ausflüge (am 31. Tag flog ein Exemplar unter

Mitnahme eines Kokonbodens aus, am 32. bereits vier weitere, und am 33. unternahmen sämtliche Individuen Ausflüge. Einige dienten als Wache). Beginn der Feldarbeiten. (In der Zeit vom 34. bis zum 37. Tag Wandlung von der „Hausangestellten" zur Feldbiene. Am 34. Tage verlies die erste Biene das Nest zur Einsammlung von Nektar.)

e) *Vom 36. bis 49. Tag:* Reinigungsarbeiten, Herausschaffen von allerlei Material (37. Tag). Feldtätigkeit (drei weitere Arbeiterinnen wurden am 37. Tag zu Feldbienen; am 38. jedoch sämtliche. Es konnte keine Beziehung festgestellt werden zwischen den ersten zu einem höheren Arbeitsalter übergewechselten Bienen und den ersten, welche zu Feldbienen wurden. Gewöhnlich sammelten sie Pollen von 8^{30} h bis 12^{30} h und Nektar von 11^{00} h bis 18^{00} h. Am 36. Tag wurde das letzte Mal eine Biene bei Inkubation beobachtet, am 42. Tag das letzte Mal bei Nektarannahme, der letzte Termin für beobachtete Wachsarbeiten fällt auf den 36).

3) Unter Vergleich der Arbeitsteilung bei *Apis mellifera* L. mit *Bombus agrorum* (Fab.) schließt der Author, daß *Melipona* mehr zu *Apis* verwandt ist, allerdings bestehen zwei größere Unterschiede: a) Bei *Melipona* ist die Wachsperiode weiter ausgedehnt; die Haupttätigkeitsperiode liegt früher als die für die Zellfüllung (Nahrung) vorgesehene Periode, während es bei *Apis* gerade umgekehrt ist; b) *Apis*-arbeiterinnen verlassen das Nest, sei es zur Arbeit oder Gelegenheits-flügen, in einem wesentlich früheren Stadium als *Meliponen*-Arbeiterinnen.

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LE DÉCLENCHEMENT ET LA RUPTURE DE L'ÉTAT D'HIBERNATION CHEZ *CREMASTOGASTER SCUTELLARIS* OL. *(HYMENOPTERA - FORMICOIDEA)*

par

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Nous avons observé depuis longtemps déjà que la Fourmi *Cremastogaster scutellaris* forme de grandes colonnes de récolte, formations stables pendant toute une saison. Dans une note précédente (1) nous avons montré qu'il est relativement facile d'étudier l'activité collective des ouvrières hors du nid en faisant varier les facteurs du milieu et en observant le comportement de ces colonnes. Il nous a été ainsi possible de déterminer l'existence d'un thermo-preferendum (situé aux environs de 25° pour cette espèce), pour lequel l'activité de la colonne est maxima. De même nous avons pu montrer que l'activité journalière de ces colonnes est arythmique et se trouve uniquement sous l'influence directe et mesurable de la température.

Dans l'étude qui suit, nous avons cherché à savoir de quelle façon les facteurs externes déterminaient l'arrêt d'activité hivernal (hibernation) et la reprise d'activité printanière (rupture d'hibernation) des fourmilières de *Cr. scutellaris*. Nous ne nous occuperons pas ici de ce qui se passe à l'intérieur de la fourmilière ni des incidences de l'hibernation sur le cycle biologique de la colonie (ceci fera l'objet de publications ultérieures), mais simplement des phénomènes qui sont visibles à l'extérieur du nid et qui affectent les colonnes d'ouvrières.

LE DÉCLENCHEMENT DE L'HIBERNATION

A la fin de l'automne ou au début de l'hiver (selon les conditions climatiques locales du lieu d'observation) les ouvrières de *Cr. scutellaris* cessent 'progressivement de constituer des colonnes régulières et à partir d'un certain moment on ne trouve plus aucune ouvrière hors du nid.

Cette cessation d'activité extérieure paraît *a priori* être due à un abaissement de la température.

(1) J. Soulié, Facteurs du milieu agissant sur l'activité des colonnes de récolte chez la fourmi *Cremastogaster scutellaris* OL. (*Hymenopt. Formic.*), *Insectes Sociaux*, t. II, n° 2.

Cependant nous avons remarqué, en étudiant de façon générale l'action de la température sur l'activité, qu'il n'y a plus d'activité collective (colonnes de récolte) pour cette espèce quand la température s'abaisse au-dessous de 7°. Quand la température repasse au-dessus de 7°, l'activité reprend peu à peu en suivant la courbe des températures pour arriver à son maximum à 25°.

1° **Observations.** — Or, au laboratoire, des fourmilières de *Cr. scutellaris* et d'une espèce voisine *Cr. auberti* sont entrées en hibernation alors que la température ne s'est jamais abaissée au-dessous de 12°,5. En période d'été les colonnes sont encore actives pour cette température (activité réduite, mais mesurable). De plus, quand les températures passaient au-dessus de 12°,5, l'accroissement d'activité ne suivait plus la courbe des températures comme dans le cas général, mais au contraire, de jour en jour, l'activité diminuait.

2° **Expérimentation.** — Le 15 octobre 1953 est récoltée une fourmilière de *Cr. scutellaris*, composée d'un grand nombre d'ouvrières (plusieurs centaines), de ♀ et de ♂ ailés, de couvain (larves à tous les stades) et de jeunes imagos d'ouvrières non encore pigmentées.

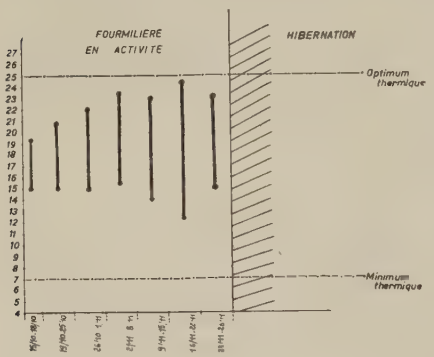


Fig. 1. — Déclenchement de l'hibernation.

En ordonnées : Échelle des températures en degrés centigrades.

En abscisses : Dates.

L'extrémité inférieure du gros trait plein correspond au minimum de température pour la durée de temps portée en abscisses. L'extrémité supérieure, au maximum de température pour la même période de temps.

Au moment de la récolte de la fourmilière et dans les premiers temps de leur vie en élevage au laboratoire, les ouvrières manifestent une activité normale : nombreuses sorties pour récolte de sucre, transport d'eau, etc. (cependant dans les élevages les ouvrières ne forment pas de colonnes, étant donné le manque d'espace).

Peu à peu, cette activité initiale se ralentit et, le 26 novembre 1953, la fourmilière est en hibernation : ouvrières groupées, serrées les unes contre les autres autour des ♀ (encore ailées ou déjà désailées) et du couvain, sous des écorces ou des abris divers que nous leur avions fournis.

Tableau des maxima et des minima de température relevés par thermomètre enregistreur depuis la récolte de la fourmilière jusqu'à l'entrée en hibernation.

(Les températures sont relevées par période d'une semaine, le premier chiffre entre parenthèses indique la température maxima et le second la température minima, relevées sur la feuille d'enregistrement thermique pour la semaine.)

Date de récolte : 15 octobre.

15	octobre	1953	—	18	octobre	1953	: (19°,5 — 15°) ;
19	—	—	—	25	—	—	: (21° — 15°) ;
26	—	—	—	1er	novembre	—	: (22° — 15°) ;
2	novembre	—	—	8	—	—	: (23°,5 — 15°,5) ;
9	—	—	—	15	—	—	: (23° — 14°) ;
16	—	—	—	22	—	—	: (24°,5 — 12°,5) ;
23	—	—	—	26	—	—	: (23° — 15°).

Date d'entrée en hibernation : 26 novembre 1953.

Nous remarquons que, pour cette période du 15 octobre au 26 novembre, la température n'est pas passée une seule fois par l'optimum thermique : 25° pour cette espèce (fig. 1).

Ainsi donc la fourmilière est entrée en hibernation sans que le minimum de température ait atteint 7°, température qui normalement (en période estivale) conditionne la cessation d'activité. On pouvait donc penser que le phénomène d'hibernation n'était pas dû à une action « simple » de la température.

LA RUPTURE DE L'HIBERNATION

Ce phénomène a été étudié expérimentalement au laboratoire, et les résultats de l'expérimentation ont été confirmés par des observations dans la nature.

1° **Essais au laboratoire.** — Sur la colonie de *Cr. scutellaris* en hibernation depuis le 26 novembre sont prélevées 100 ouvrières environ, qui sont installées dans un appareil d'élevage séparé (bouturage artificiel). Après vingt-quatre heures de délai, nécessaires pour apaiser les perturbations causées par le bouturage, cette petite colonie est de nouveau dans l'état caractéristique de l'hibernation (ouvrières groupées les unes contre les autres dans des trous d'écorce, ne manifestant aucune activité de recherche de nourriture et d'eau). Nous avons laissé cette colonie bouturée à la température du laboratoire jusqu'au 25 janvier 1954.

Tableau des températures du 26 novembre 1953 au 25 janvier 1954.

(Mêmes indications que pour le tableau précédent.)

Date d'entrée en hibernation : 26 novembre 1953.

26	novembre	1953	—	29	novembre	1953	: (21° — 15°,5) ;
30	—	—	—	6	décembre	—	: (17°,5 — 12°,5) ;
7	décembre	—	—	13	—	—	: (22° — 16°) ;
14	—	—	—	20	—	—	: (21° — 14°) ;
21	—	—	—	27	—	—	: (20° — 10°) ;
28	—	—	—	3	janvier	1954	: (16° — 6°) ;
4	janvier	1954	—	10	janvier	—	: (19° — 10°,5) ;
11	—	—	—	17	—	—	: (20°,5 — 9°) ;
18	—	—	—	24	—	—	: (22°,5 — 13°).

A cette date du 24 janvier, aucune modification ne s'est produite dans l'état d'hibernation de la colonie.

Les essais de rupture de l'hibernation ont été effectués du 25 janvier 1954 au 30 janvier 1954 (pendant cette période, le minimum de température auquel furent soumises les fourmis en expérience fut de 9°). Les essais de rupture d'hibernation consistent à soumettre les fourmis, en étuve, à des températures égales ou légèrement supérieures à l'optimum thermique de cette espèce (25°).

Le 25 janvier 1954 : passage en étuve 24-26° pendant 5 heures.
Le 26 — — : — — — 2 —
Le 27 — — : 1er — — — 2 h. 30.
Le 27 — — : 2e — — — 3 h. 30.

Après le premier passage, deux ouvrières sont sorties de leur refuge mais restent immobiles à 1 cm environ de ce dernier. Après le deuxième passage, ces deux ouvrières ont réintégré leur refuge.

Le 29 janvier 1954 : passage en étuve 24-26° pendant 2 h. 30.
Le 30 — — : — — — 3 h. 30.

Les fourmis subirent donc six passages par l'optimum thermique sans que l'hibernation soit rompue (fig. 2).

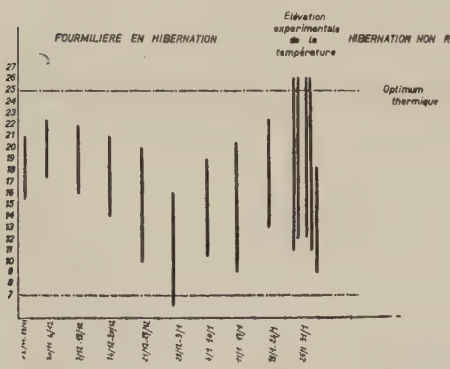


Fig. 2. — Essai de rupture expérimentale de l'hibernation. Mêmes indications que pour la figure 1.

Maintien artificiel de la fourmilière en hibernation.

Par la suite, nous avons maintenu les fourmis à la température du laboratoire jusqu'au 17 mai 1954, en veillant à ce que le maximum de température n'atteigne jamais l'optimum de 25° ; et ceci pour tenter de maintenir artificiellement l'hibernation au delà de la durée normale : en moyenne, dans la nature, cet état dure du 15 novembre au 15 mars, soit quatre mois. On verra, par comparaison avec des essais en pleine nature, que l'hibernation d'un nid de *Cr. scutellaris* a été rompue en 1954 à Toulouse à partir du 6 mars.

Tableau des températures maxima et minima du laboratoire pour la période du 1er février 1954 au 20 juin 1954, date à laquelle l'hibernation de la fourmilière en expérience fut définitivement rompue.

(Mêmes indications que pour les tableaux précédents.)

1er février 1954 — 7 février 1954 : (20° — 11°) ;
8 — — — 14 — — : (21° — 13°) ;
15 — — — 21 — — : (19°,5 — 13°,5) ;
22 — — — 28 — — : (22°,5 — 14°) ;

28 février 1954 — 7 mars 1954 : (22° — 14°) ;
8 mars — — 14 mars — : (20° — 15°) ;
15 — — — 21 — — : (20° — 15°) ;
22 — — — 28 — — : (20° — 15°) ;
29 — — — 4 avril — : (19°,5 — 15°,5) ;
5 avril — — 11 — — : (19°,5 — 12°,5) ;
12 — — — 18 — — : (17°,5 — 12°,5) ;
19 — — — 25 — — : (19° — 12°) ;
26 — — — 2 mai — : (22° — 15°) ;
3 mai — — 9 — — : (20° — 14°) ;
10 — — — 16 — — : (23° — 16°) ;
17 — — — 23 — — : (17° — 14°) ;
24 — — — 30 — — : (20°,5 — 16°) ;
31 — — — 6 juin — : (21° — 19°,5) ;
7 juin — — 13 — — : (22° — 19°) ;
14 — — — 20 — — : (22° — 20°),

Date de rupture définitive de l'hibernation : 20 juin 1954.

Les 18 mai, 20 mai, 22 mai, 24 mai, 26 mai, 28 mai, 30 mai, 1er juin, 3 juin, les fourmis sont transportées pendant une heure à l'étuve à 25-26°.

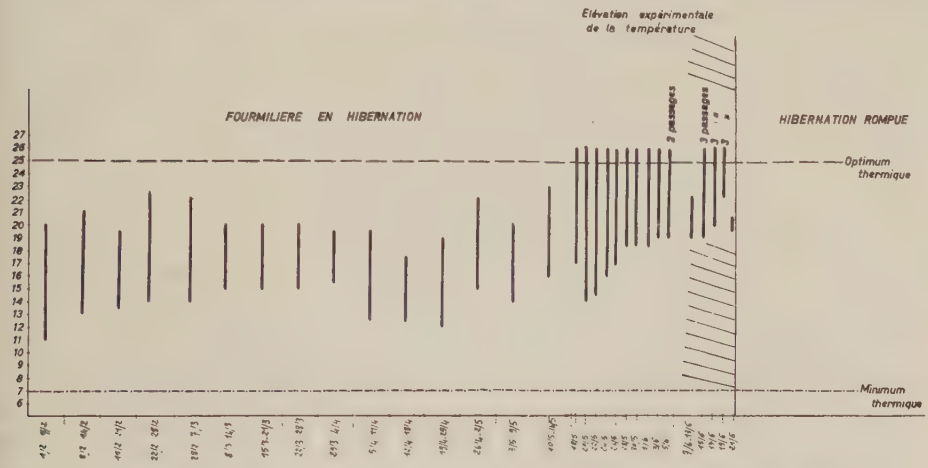


Fig. 3. — Maintien artificiel et rupture expérimentale de l'hibernation. Mêmes indications que pour les figures précédentes.

Le 5 juin, elles subissent deux passages d'une heure, séparés par un séjour de deux heures à la température du laboratoire : maximum 20°. L'hibernation n'est pas rompue. Du 6 juin au 14 juin, les fourmis restent à la température du laboratoire (avec pour cette période une température maxima de 22° et minima de 19°) sans qu'apparaisse aucun signe de reprise d'activité.

Les 15 juin, 17 juin, 19 juin, les fourmis subissent journellement trois passages d'une heure à l'étuve à 25-26° (chaque passage séparé du suivant par un séjour d'une heure à la température du laboratoire). Le 21 juin,

après vingt passages par l'optimum thermique, l'hibernation est rompue définitivement, et les ouvrières manifestent une activité normale qui ne cessa pas par la suite (fig. 3). Dans cet essai, les fourmis passèrent donc en état d'hibernation une période de sept mois (du 26 novembre 1953 au 20 juin 1954), soit près du double de la durée normale.

2° **Observation sur nid de** *Cr. scutellaris* **dans la nature. Étude de la rupture de l'hibernation :**

	Maximum de température.	Minimum de température.
23 février 1948	35°	0°
	(Soit dans la journée 2 passages par l'optimum thermique.)	
24 — —	38°	4°
	(2 passages par l'optimum.)	
25 — —	17°	3°
26 — —	27°	7°
	(2 passages par l'optimum.)	
27 — —	25°	6°
	(1 passage par l'optimum.)	
28 — —	30°	3°
	(2 passages par l'optimum.)	
1er mars —	23°	2°
2 — —	32°	3°
	(2 passages par l'optimum.)	
3 — —	35°	1°
	(2 passages par l'optimum.)	
4 — —	25°	5°
	(1 passage par l'optimum.)	
5 — —	13°	4°
6 — —	24°	1°

Le 6 mars, après 14 passages par l'optimum (depuis le début des mesures), 2 ouvrières sont trouvées circulant sur la piste.

7 mars 1954	30°	0°
	(2 passages par l'optimum.)	

Aucune fourmi sur la piste.

8 mars 1954	33°	2°

Plusieurs fourmis (une dizaine environ) circulent lentement sur la piste après 18 passages par l'optimum.

9 mars 1954	28°	4°
	(2 passages par l'optimum.)	

Pas de fourmis hors du nid.

10 mars 1954	14°	2°

Bien que le maximum de température n'ait pas dépassé 14°, plusieurs fourmis circulent sur la piste après 20 passages par l'optimum.

11 mars 1954	33°	4°
	(2 passages par l'optimum.)	

Plusieurs fourmis circulent sur la piste, la colonne de récolte commence à s'organiser. A partir de cette date, il commence à être possible de mesurer l'activité de la colonne. L'hibernation peut être considérée comme définitivement rompue, après 22 passages par l'optimum thermique (fig. 4).

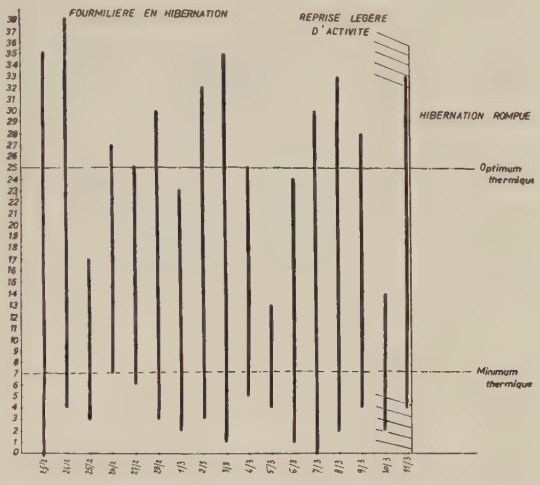


Fig. 4. — Rupture naturelle de l'hibernation. Mêmes indications que pour les figures précédentes.

Interprétation des observations et des premiers résultats expérimentaux.

1° Le facteur principal déterminant le déclenchement ou la rupture de l'hibernation est la température extérieure.

2° Cette température n'agit pas de façon simple et absolue. Le déclenchement de l'hibernation n'est pas automatiquement entraîné par le passage par un minimum de température déterminé correspondant à la température pour laquelle l'activité est normalement nulle (7° pour *Cr. scutellaris*) ; de même que la rupture d'hibernation n'est pas causée par le passage par un maximum de température déterminé lui aussi.

3° L'hibernation se déclenche, après une réduction progressive de l'activité, si les fourmis ne sont pas soumises durant un certain temps à la température optima, déterminant le maximum d'activité dans des conditions normales (25° pour *Cr. scutellaris*). De même l'hibernation est rompue après une série de passages de la température par cet optimum thermique, et ceci, quelle que soit la température minima à laquelle ces fourmis ont, entre temps, été soumises.

En conclusion, nous pouvons formuler une hypothèse touchant le mode d'action de l'optimum thermique sur le déclenchement et la rupture de l'état d'hibernation chez l'espèce de fourmi étudiée.

Le passage ou les passages journaliers de la température par l'optimum thermique (1) donnent à l'activité des fourmis une « impulsion » (nous proposons de nommer ce phénomène : « impulsion thermique ») nécessaire et suffisante pour maintenir l'activité jusqu'au passage suivant par l'optimum (correspondant au maximum d'activité).

Pendant le printemps, l'été, l'automne, les passages par l'optimum sont suffisamment fréquents pour qu'il n'y ait pas interruption totale de l'activité [sauf au-dessous du minimum absolu (1) : 7° ou au-dessus du maximum

(1) J. Soulié, Facteurs du milieu agissant sur l'activité des colonnes de récolte chez la fourmi *Cremastogaster scutellaris* OL. (*Hymenopt. Formic.*), *Insectes Sociaux*, t. II, n° 2.

absolu : 44° pour cette espèce] ; et cette activité est alors directement fonction de la température.

Puis vers le début de l'hiver, les passages par l'optimum se font moins fréquents, l'impulsion est moindre, l'activité se ralentit et, au bout d'un certain temps, il n'y a plus de passage du tout par l'optimum ou à des intervalles de temps si éloignés que l'activité devient nulle. C'est l'état d'hibernation tel que nous l'avons défini au début de cette note.

Inversement, à la fin de l'hiver ou au début du printemps, les passages par l'optimum se font de plus en plus fréquents, finissent par devenir journaliers ; les impulsions thermiques se répètent à des intervalles de plus en plus brefs et, au bout d'un certain nombre de passages par l'optimum, l'activité se déclenche à nouveau, se régularise peu à peu pour ne plus dépendre ensuite que de la courbe des températures, et ce, de façon directe. L'hibernation est rompue.

NEW PARASITIC ANTS OF THE GENUS *KYIDRIS*, WITH NOTES ON ECOLOGY AND BEHAVIOR

by

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During the course of a collecting and study tour of New Guinea made by one of us (Wilson) early in 1955, there were discovered on several occasions at different localities remarkable mixed nests, each composed of two widely different species of dacetine ants. The larger of the two different kinds found mixed was always *Strumigenys loriæ* Emery, a common New Guinea species peculiar in its own right because of its frequently highly polymorphic worker caste (Szabó, 1910). The smaller of the two nestmates proved to belong in each case to the genus *Kyidris*, a smithistrumiform entity previously known only from Japan and Formosa. Close study has revealed that the New Guinea *Kyidris*, while unmistakably congeneric with the Japanese species, is not of the same species. Furthermore, the aberrant females of the New Guinea samples indicate that at least two different species, both new, are contained in the collection. It is the purpose of this paper to review briefly the present status of *Kyidris*, to describe and name the new species of the genus, and to describe the behavior and ecology of the mixed colonies as observed in the field and in the artificial nest.

THE GENUS *KYIDRIS* BROWN

Kyidris and its monobasic genotype, *K. mutica* Brown (1949) were first described on the basis of a handful of workers collected by H. Okamoto on Shikoku and sent to Dr. Keizô Yasumatsu, of the University of Kyushu. Dr. Yasumatsu recognized these workers as belonging to a new species of the tribe Dacetini near the genus *Smithistruma* Brown, and sent them to Brown for description. Comparison with various dacetine genera showed that structurally *K. mutica* is most closely related to the short-mandibulate genera *Serrastruma* Brown (Africa), *Smithistruma* (widespread) and *Weberistruma* Brown (Oriental Region), but that it differs from all of these in the structure of the head and mandibles and, above all, in the high, rounded, bipartite and unarmed alitrunk.

In an addendum to the same paper in which *K. mutica* was first described from the workers (Brown, 1949), a female belonging to the genus was described as a new species (*K. nuda* Brown) from a single Formosan specimen. This specimen was rather small to fit comfortably as the female caste of *K. mutica*, and it showed reduction of nodal and gastric

sculpture, obsoleteness of the spongiform appendages, modified form of petiolar node and loss of erect hairs as compared to the *K. mutica* workers. Despite these strong differences, unusual for the female-worker separation of dacetines, Mr. Okamoto subsequently was able to associate females matching *K. nuda* with workers of *K. mutica* by rearing further Japanese material. Through the cooperation of Dr. Yasumatsu, it was possible to synonymize *K. nuda* under *K. mutica* (Brown, 1952) with a reasonable degree of certainty. It is worth noting that the nests of *K. mutica* were found on Shikoku " ... in the clay soil of somewhat arid place... " and that they were apparently composed entirely, so far as the samples went, of the single species *mutica*. Azuma has found *K. mutica* not uncommon in southeastern Honshu, and we have been able to confirm these records from two workers sent from Azuma's collection. We therefore now know *K. mutica* from central Japan and from Formosa. Though we have no direct reason to consider the biology of this species to be unusual, the fact that the queens are slightly aberrant, and the discovery that the two new Papuasian species described below are parasitic in the nests of *Strumigenys loriae*, lead one to suspect that *K. mutica* may be a temporary social parasite of some species of *Strumigenys* in Japan. By far the most likely candidate as a host is *S. lewisi*, the commonest Japanese species of the genus, and it may be profitable for some Japanese experimenter to try raising *K. mutica* fertile dealates in *S. lewisi* nests. In Formosa, *S. formosensis* Forel is the common *Strumigenys* in most parts. It must be emphasized that a parasitic role for *K. mutica* is at present purely speculative.

The two new species described below from Papua and New Guinea are undoubted members of the genus *Kyidris*. Not only is the *K. media* queen intermediate in size, habitus and sculpture between those of *K. mutica* and the extremely aberrant *K. yaleogyna*, but the workers of all three species are so nearly identical, except in trivial and not very constant characters of size, sculpture and pilosity, that without the accompanying females they might have been assigned to one species. In fact, four stray workers (Accession No. 917) from the lower Busu River, New Guinea, only a few miles from the type locality of *K. media*, are in several ways more like *mutica* than like *media*; without the associated female caste, we cannot say what they are.

As is described in some detail farther below, the Papuasian species definitely show inquilinous behavior and, so far as we know at present, are obligatory in this behavior. Although we have no direct evidence for parasitic nest-founding by the queens, the characteristics shown by this caste indicate strongly that they normally initiate a new colony by entering either a pure colony of the host *Strumigenys* or a mixed colony consisting of *Strumigenys* and their own species, which may thereupon divide by "swarming." If this correspondence really holds, then we might expect to find, following the degree of specialization shown by the females structurally, that *K. yaleogyna* is more specialized in a parasitic direction than is either of its congeners.

A peculiarity of *Kyidris* workers that shows much more strikingly in life than in dead, mounted material is the disproportionate length of the legs, especially noticeable when comparison is made against *Smithistruma* and other close genera. What the function of long legs might be in this case is hard to understand; perhaps one advantage is an enhanced ability to reach higher from the base level, the better to engage in "theft trophallaxis" from host pairs exchanging food (*vide infra*).

THE SPECIES OF *KYIDRIS*

In the descriptions to follow, the abbreviations used for measurements and indices are those of the recent series of studies on the dacetine ants

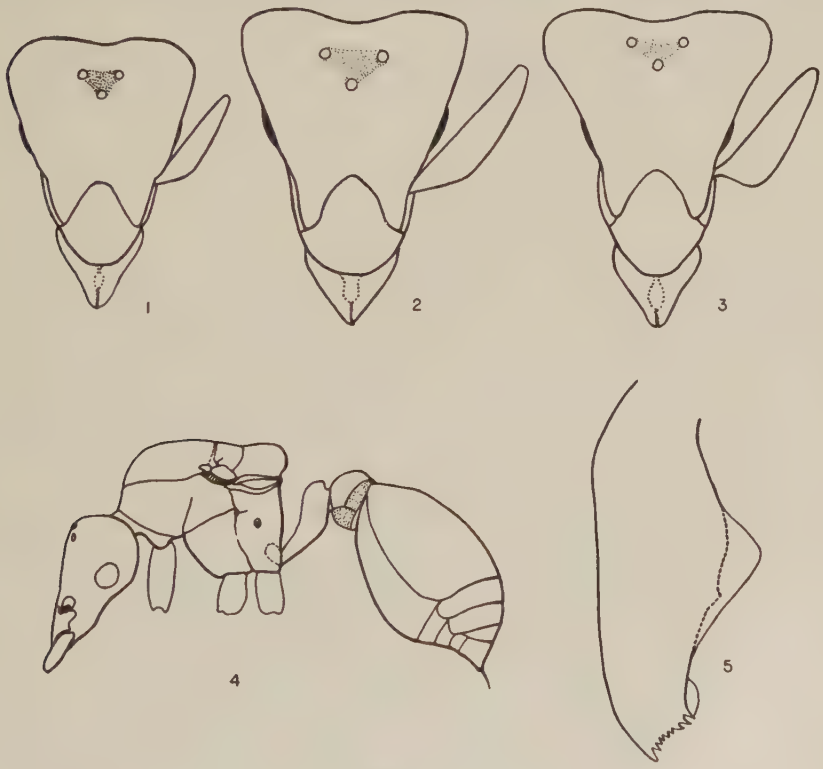


Fig. 1 à 5.

(see especially Brown, 1949, 1953). The letter "L" used alone or in combination always signifies a maximum measurable length in millimeters. TL is the sum of the axial lengths of the various sections of the body from the tip of the closed mandibles to the gastric apex. HL is the maximum length of the head, including occipital lobes and clypeus, but excluding mandibles. WL is the maximum measurable length, in side view, of the

alitrunk, anterior neck excluded. The letter "I" signifies an index, or percentage relationship of two dimensions. CI, the cephalic index, is the maximum width of the head expressed as a percentage of HL, while MI, or mandibulo-cephalic index, is the length of the exposed portion of the closed mandibles as seen from dorsal view, expressed as a percentage of. HL.

The two new species, *K. yaleogyna* and *K. media*, are based upon females as holotypes, as well as on paratype material of female worker and male castes from the same and other nests from the same localities respectively. All of the Papuasian material was collected by WILSON, and the holotypes from it, together with ample paratype series, will be deposited in the Museum of Comparative Zoology, Harvard University. Other paratypes will be deposited in the Museo Civico di Storia Naturale of Genoa with the Emery Collection, in the United States National Museum, and in one or more public Australian collections.

For *K. mutica*, we have provided an up-to-date synonymy and enough descriptive material to permit a comparison with the new species.

Kyidris mutica Brown.

Kyidris mutica Brown, 1949, Mushi, 20 : 3-6, fig. 1, worker. Type locality: Hirooka, Kamino-mura, Agawa-gun, Tosa Prov., Shikoku, Japan, 30 M. altitude.

Kyidris nuda Brown, 1949, ibid., pp. 23-24, female. Type locality: Mt. Niitaka, Formosa ; synonymy by Brown, 1952, Psyche, 58: 124.

Polyhomoa itoi Azuma, 1950, Hyogo Biology, 1: 35-37, figs., worker. Type locality: Tomogashima, Kii Prov., Japan. Synonymy by Brown and Yasumatsu, 1951, Mushi, 22: 93-95.

Kyidris itoi Creighton, 1950, Psyche, 54: 93-94.

Female : The measurements and indices of the *K. nuda* holotype are taken from the original description: TL 2.21, HL 0.57, WL 0.61 mm.; CI 77, MI 19. Two specimens from the reared Shikoku nest (see under male, below) are even smaller, with HL 0.54-0.55 mm.

Head shape as in fig. 1. Sculpture as in the worker and as in normal *Smithistruma*, etc. females, i. e., reticulate-punctulate over most of head and alitruncal dorsum; however, the sculpture is shallower than usual, in some places feebly shining, and is replaced by smooth, shining areas on the nodes. As in the other *Kyidris* females, the specialized paired erect hairs are absent from the dorsum. The discrepancy in size between this female and its workers is much smaller than that between the respective castes of the Papuasian species, and the sculpture is more nearly normal, but this female still shows a distinct tendency to vary in the direction of the Papuasian forms.

Worker: The type series measured TL 2.00-2.15, HL 0.50-0.54, WL 0.53-0.56 mm., and the indices were CI 76-80 and MI 21-24. A second Shikoku

collection, from the same colony as the males described below and two workers from southeastern Honshu, are about the same in size and proportions. The pairs of large remiform ("oar-shaped") hairs, one pair each on occiput, mesonotum, petiole, postpetiole, anterior gastric dorsum, and several pairs farther back, do seem constant in number and position in this material.

Male: Smaller than the males of the Papuasian species; HL 0.45, forewing L ca. 2.2 mm. Measurement and description from 2 specimens collected by H. Okamoto at Moriyama-mura, Agawagun, Tosa Province, Shikoku, and reared from a nest together with females and workers. Mandibles short, straight, rudimentary, tapering to a simple acute point; it seems that there is no possibility that they can close to meet each other. Postpetiole shining in front, vaguely striolo-punctulate behind; postpetiolar collar reduced to a transverse posterior rudiment, present only in the middle. Genitalia retracted, not examined. Color, except the blackish head, generally lighter, more brownish yellow than in Papuasian species, but it is not certain that this is the full adult pigmentation.

Azuma (*loc. cit.*) found colonies containing up to 1000 workers nesting in "plant cavities", but other notes he gives on these collections are not clear in the translation available.

Kyidris yaleogyna sp. nov.

Female: holotype, alate: TL 3.1, HL 0.70, WL 0.81, forewing L ca. 2.9 mm.; CI 80, MI 16. *Ex* colony no. 610. Paratypes, alate and dealate, TL 3.0-3.2, HL 0.69-0.72, WL 0.81-0.85; CI 79-81, MI 16-17. Two specimens *ex* colonies nos. 610 and 664.

Much larger than its own workers and the queens of *K. mutica*. Head as in fig. 3; the most significant characters of gross outline are the relatively narrow anterior cranium, accompanied by a decided concavity of the converging sides in front of the occipital angles, causing the angles themselves to appear more prominent laterally, and the broadened, anterobasally sublobose antennal scapes.

Mandibles like those of the worker and the new species, *K. media*, shown in fig. 5, but smaller relatively than in the worker and with a reduced number of teeth in the apical series. The size of the individual teeth is reduced toward the middle of the series, and there are only 6 (perhaps a seventh minute tooth is present in some specimens, but the holotype has 6) teeth in addition to the apical tooth proper. Another odd character found in the females of both *yaleogyna* and *media*, but never in the *K. mutica* female or in the workers of any of the three known species, is the low, rounded, transparent lobe situated in the great diastema just proximal to the first tooth of the apical series. In all known *Kyidris* workers, and in the *K. mutica* female, the dentition is alike, consisting of apical plus 11 teeth in the apical series, all rather uniform in size except the first (basalmost) tooth, which is slightly larger (Brown, 1949, fig. 1c).

The alitrunk is even higher and bulkier relatively than in *K. mutica*, and the scutellum projects somewhat to overhang the vertical feebly angled free face of the propodeum. Petiole slightly more massive (deeper) than in *K. mutica*, rounded above and below and with no traces of spongiform appendages. Postpetiole evenly rounded, its spongiform appendages reduced to a heavy, glassy, transparent collar extending around the posterior border and down each side behind, and a fair-sized ventral lobe of the same consistency. Gaster bulky, its dorsal surface smooth, without basal sculpturing of any kind.

Entire body, including most of the appendages, smooth and shining, with a few scattered indistinct punctures on the head, becoming deeper and more elongate on the clypeal surface beneath each of the hairs, and also on the mandibles. In dealate females, however, the integumental surface is normally covered by a continuous sheet of transparent material, apparently a secretion, that renders the surface opaque to subopaque, and sometimes even rough, where it lies.

Ground pilosity very sparse, consisting of small, fine appressed hairs on dorsum of head and alitrunk, mostly directed obliquely mesad; denser and somewhat heavier appressed linear hairs on clypeus, underside of head, mandibles and scapes. Very fine small appressed hairs scattered over gastric dorsum and apex, directed caudad. Erect hairs absent except for a few fine ones at the gastric apex. Color clear light ferruginous, gaster sometimes a trifle darker; appendages more yellowish; ocellar triangle blackened.

Worker: paratypes: TL 2.2-2.4, HL 0.53-0.59 (0.56), WL 0.55-0.61 mm.; CI 78-82 (80), MI 22-24. Measurements from 14 specimens from 3 different nests. Similar in most respects to the worker of *K. mutica*, but usually slightly larger and a bit darker, with head not quite so thick dorsoventrally, and the node proportionately larger and deeper, though all of these characters show variation in both species. The best distinguishing character appears to be the pilosity. In *yaleogyna*, the appressed ground pilosity is finer on the head and scapes, but coarser and more conspicuous on the nodes and gaster. The paired erect remiform hairs of the occiput, mesonotum and gaster are generally smaller and less conspicuous in *yaleogyna*, and on the occiput especially, they may be missing altogether or else appressed. On the nodes and anterior gastric dorsum, the paired remiform hairs found there in *mutica* are absent or else not clearly differentiated from the surrounding short ground hairs, but even so, *yaleogyna* workers occasionally have one or two of the remiform nodal hairs enlarged, fairly distinct from the rest, and weakly raised.

Basal costulation of gaster interspersed with reticulation, rendering the surface here subopaque to opaque, and extending back to between 1/2 and 2/3 the length of the first gastric segment, or farther than in *mutica*, in which species the costulation rarely extends as far as halfway, and usually ends far short of halfway. The color is a medium to light ferruginous yellow.

Male: paratypes: TL 2.79, HL 0.54, L head with closed mandibles 0.61, head width including eyes 0.45, without eyes 0.41, WL 0.80, forewing L about 2.75 mm. Measured from a single specimen from colony no. 664; another male from colony no. 647 is slightly larger, HL 0.56 mm.

General habitus as in male of *Smithistruma*; propodeal teeth not developed. Mandibles reduced and slender compared to female and worker of the same species, but curved inward and capable of meeting; apical tooth followed basad by apical series of one to about four teeth, varying with the individual specimen, the teeth followed basad by a variable diastema and a basal lamella more or less like that of the female and worker. Head, alitrunk and appendages densely reticulo-punctulate and opaque, as in *Smithistruma*, and with similar but somewhat effaced sculpture on petiole; postpetiole with dorsal surfaces usually largely smooth and shining, at least in front, its posterior lamelliform collar fairly well developed, projecting as a rim and widened at the sides; no ventral appendages developed.

Pygostyles robust, with long slender hairs. Exserted parameres thick, curving gently mesad, with narrowly rounded apices, their outer (dorsolateral) faces shallowly impressed; mesial borders cultrate, lateral border convex. Volsellae (not removed for flat view) appearing much like those of *Smithistruma lamellignatha* Brown seen in place, i. e., the digitus is straight and slender.

Color blackish-brown, shading to a lighter, usually more yellowish-brown on mandibles, appendages and gastric apex. Forewing with the usual reduced venation of the smaller dacetite genera, only ScR, stigma, basalis, A and r fairly distinct; Rs, M and CuA represented by grooves. Hindwing straplike, with a single short anterior vein in the basal half; hamuli 4, near midlength of wing.

The wings are much alike in all three species and both sexes of *Kyidris* so far seen, except that larger specimens, and especially the females, have the weakest veins slightly better defined than in smaller specimens, in which veins like Rs and M tend to disappear completely. The 4 hamuli are constant in size and position in both sexes of all three species; the units decrease in size apicad.

The holotype (from nest no. 610) and numerous paratypes of all castes were taken from three separate mixed nests with *Strumigenys loriae* (nos. 610, 647, 664) found at Bisianumu, near Sogeri, Papua, at approximately 500 M. altitude in rainforest, March 15-20, 1955 (E. O. Wilson).

Kyidris media sp. nov.

Female: holotype, alate: TL 2.9 (corrected for gastric extension), HL 0.67, WL 0.75, forewing L ca. 2.7 mm. ; CI 82, MI 17. Very similar to *K. yaleogyna* in general habitus and in form of alitrunk, but different in its smaller size; in the shape of the head (fig. 2), which is not so strongly

narrowed anteriorly, and has more nearly straight sides; in the form of the antennal scapes, which are slightly less broad overall and which lack the sublobose broadening of their bases; and in the distinct sculpturing of considerable areas of the body. Mandible as in fig. 5.

Dorsum of head behind clypeus superficially and rather irregularly punctulate-striate in a longitudinal direction, subopaque. Alitrunk indefinitely coriaceous or finely punctulate in large part, weakly shining, the superficially sculptured areas merging into the smoother and more shining discal portions of scutum and pleura. Nodes, gaster and center of occiput for the most part smooth and shining, but the basal half of the first gastric tergum bears very fine, dense, superficial interrupted costulation radiating outward from its basal margin, rendering the surface here subopaque. Legs and antennae very finely punctulate to smooth, generally shining. The postpetiolar appendages are more reduced than those of *yaleogyna* female, consisting in *media* female of only a very narrow semitransparent collar above and a more or less tuberculiform vestige beneath. Pilosity and color similar to those of *yaleogyna* female.

Worker: paratypes: TL 2.2-2.3, HL 0.54-0.57, WL 0.56-0.61 mm.; CI 82-84, MI 23-24. Measurements from two specimens from type nest.

Very similar to the worker of *yaleogyna*, but has the erect paired remiform hairs even more strongly reduced, these being entirely absent from the occiput, nodes and anterior gaster, while the mesonotal and posterior gastric pairs are very small, fine and inconspicuous. However, if the workers from the nearby Busu River locality (no. 917, see below) should prove to belong to this species (*media*), then the pilosity diagnosis would have to be broadened considerably.

Base of gaster above with very fine, sericeous-opaque reticulo-striolation, longitudinally arranged and extending back 2/3 or more of the length of the basal segment, after which the remainder of the gaster is smooth and shining. The usual coarse costulae, still distinct in *mutica* and *yaleogyna*, are reduced to elements so fine in *media* worker that they are merged with the fine reticulate background or intercalary sculpture.

Male: paratype: A single specimen from the type nest series closely resembles the *K. yaleogyna* male, but averages a little smaller, HL 0.51, forewing L ca. 2.4 mm. Posterior lamelliform collar of postpetiole reduced to a very narrow fringing border. Smooth patch on anterodorsal postpetiole restricted in size. The mandibles and exserted genitalia (the latter not dissected) seem to fall within or very close to the range of variation of *yaleogyna*.

The holotype, together with an additional alate female paratype, one male paratype, and six worker paratypes (plus a few additional workers) were taken from a mixed nest (no. 713) with *Strumigenys loriae* at Didiman Creek, near Lae, Australian Mandated Territory of New Guinea, in lowland rainforest, March 29, 1955 (E. O. Wilson).

Kyidris sp.

Four stray workers, sample no. 917, from the lower Busu River, Huon Peninsula, New Guinea, are very small in size: HL 0.45-0.47 (one specimen of the four is headless), WL 0.46-0.48 mm.; CI 77-81. Paired remiform hairs present and well developed on occiput, mesonotum and anterior gastric dorsum, in addition to the posterior gastric pairs. On nodes, pilosity generally much reduced, virtually absent, no large paired remiform hairs. Basigastric costulation dense and reticulated, but ending abruptly before the middle of the first segment.

These are the smallest *Kyidris* workers we have seen from anywhere, smaller even than the Japanese samples. Whether they are merely variant specimens, perhaps nanitics from an incipient nest, of *K. media*, or are representatives of a third Papuasian species, cannot be decided from the present material. It is clear that in this genus, we should be unwise to describe a new species in the absence of the female caste.

ECOLOGY

Kyidris yaleogyna. ACCESSION NO. 610. Bisianumu, Papua; March 17, 1955. Foothills rain forest, relatively undisturbed. The mixed *S. loriae—K. yaleogyna* colony occupied the terminal 18 inches of a large, rotting, moss-covered log lying on the ground at the edge of a small clearing. The wood was "rich-red", at the stage where passalid beetles are typically very prevalent, and except for several central shafts of resistant hardwood, it could be crumbled easily in the hands. The log was removed almost intact to a sheltered place and the colony divided into convenient lots and counted. That this colony is by far the largest recorded for the tribe Dacetini is shown by the following figures, which of course still include only those individuals in the nest at the time it was gathered. *Strumigenys loriae*: 1622 workers, 16 dealate queens. *Kyidris yaleogyna*: 1170 workers, 4 dealate queens, 84 alate queens, 51 males The large number of parasitic workers, almost equaling that of the host workers, is of especial significance and will be commented upon later.

Abundant brood in all stages of development was present, with no obvious numerical predominance of any stage. This filled several dozen well-defined galleries and chambers over an area of a cubic foot or more. Host and parasite pupae (other stages are not readily determinable) were mixed together everywhere; those of the host were somewhat more abundant. The dealate queens of both genera were distributed throughout the brood area. In one chamber a *Strumigenys* and *Kyidris* were found side by side, but the other 18 queens were all taken singly. Nearly every chamber and gallery contained *Strumigenys* and *Kyidris* workers mingling amicably. In some of these cavities the proportions of the two genera

were about equal, but in others there was definite evidence of segregation, i.e. one or the other preponderated almost to the exclusion of the other. This segregation seems to have been at least in part a temporary effect of the different "temperaments" of the two species. When the nest was disturbed, the *Strumigenys* showed a tendency to gather together in cavities back from the broken parts of the log, where they remained quiescent, whereas the *Kyidris* were very restless, wandering steadily from chamber to chamber and only infrequently settling in one spot. The dealate queens showed no particular preference for "segregated" groups of their own species, but were evidently randomly distributed. Not enough pupae were present to determine with certainty whether there was any tendency for species-separation in the brood, but it was WILSON's impression that there was not.

After the nest had been dissected in the field, WILSON established a small section in an artificial nest for further study of behavior and air-mailed another section to BROWN in the United States for independent study.

ACCESSION NO. 664. Bisianumu, Papua; March 18, 1955. This mixed colony was smaller than the one described above. It was nesting in the cavities of part of a spiny *Myrmecodia* pseudobulb lying on the ground. The pseudobulb had obviously fallen from the tree canopy above and had been on the ground for some time. Its undersurface had begun to decay and mingle with the underlying humus, and the portion of branch which had fallen with it had begun to decay; but the bulk of the plant, including its foliage, was still alive. Part of the pseudobulb was inhabited by the *Strumigenys-Kyidris* and part by a small colony of an undescribed species of the ponerine genus *Stictoponera*. The original arboreal inhabitants, probably consisting of a colony of *Iridomyrmex myrmecodiae* Emery, *I. scrutator* Fr. Smith, or *Polyrhachis andromache* Roger, had undoubtedly moved out shortly after the pseudobulb had fallen to the ground, leaving its chambers available for ground-dwelling ants. WILSON has observed spontaneous, emigration of *I. scrutator* out of pseudobulbs within twenty-four hours after they were brought down in the tops of felled trees (Busu River, New Guinea).

The entire dacetine colony was dissected out and the following population count made. *Strumigenys*: workers 243, dealate queens 4. *Kyidris*: 64 workers, 2 dealate queens, 31 males. Adults and brood (pupae) of both species were thoroughly mingled as in the larger colony (no. 610).

ACCESSION NO. 647. Bisianumu, Papua; March 18, 1955. A third mixed colony of *Strumigenys loriae* and *Kyidris yaleogyna* was found in a small rotting log on the ground in a well-shaded portion of the Bisianumu forest. Only a fraction of the colony was collected, and no population count was made.

Kyidris media. ACCESSION NO. 713. Didiman Creek, Lae, New Guinea; March 29, 1955. Margin of lowland rain forest. A small mixed colony was found in a slender rotting log on the ground. The bark of the log was intact and the wood still firm enough so that it could not be broken apart with the hands. Only a fragment of the colony was retrieved. A later count of this sample revealed that the *Strumigenys* workers outnumbered those of *Kyidris* by about three to one. A few alate queens and males of *Kyidris* were present in the nest, but none of *Strumigenys.* Adults and brood of both species appeared to be as thoroughly mingled as in the Bisianumu mixed colonies.

ACCESSION NO. 917. Lower Busu River, near Lae, New Guinea; May 3, 1955. Primary lowland rain forest. Four workers of an undetermined species of *Kyidris* were found foraging under a rotting log lying on the ground. No nest was found.

Food Habits

Studies on feeding behavior in colony no. 610 (mixed *Strumigenys loriae* and *Kyidris yaleogyna)* were made in the field by Wilson and later in the laboratory by Wilson and Brown independently. These ants conformed generally to the behavior already described for other dacetine species (cf. Brown, 1954), but showed two peculiarities of their own which seem to us of considerable significance.

First, strong evidence was obtained that the *Kyidris* workers attend coccids. When the nest of no. 610 was first opened, mealybugs were found clustered on rootlets penetrating the rotting wood of one of the peripheral chambers. These insects were at that time surrounded by a number of *Kyidris* workers. Within a few minutes after the chamber had been opened, two of the workers gently picked up coccids and started to carry them off into a darker part of the nest. When retrieved from the ants, the coccids were found to be living and apparently unharmed Other workers were seen soon thereafter tugging at some of the remaining coccids, but they gave up after a short time and wandered off by themselves. Several others remained motionless in place beside the coccids during the hour or so it took to excavate and explore the entire nest. They thus behaved in marked contrast to their sisters wandering all around them, and gave every impression of behaving as "guards" of the type described by Eidmann (1927) and others in temperate-zone ant genera.

Assuming that our interpretation is correct, this is to our knowledge the first recorded instance of higher dacetines attending honeydew-producing insects. There is a single record (G. E. Bodkin, in Crawley, 1916) of the primitive species *Daceton armigerum* Perty attending scale insects in British Guiana, but the habit seems to have been lost in most of the higher groups of the tribe. Certain Australian dacetines, however, do feed on sugary plant exudates (Brown, 1954).

Another interesting aspect of feeding behavior in the mixed colony was the great latitude of prey choice in comparison with that of other dacetines. At the nest site in the field *Strumigenys* workers were found carrying homeward a small midge and several very small, unidentified worms, probably either nematodes or enchytraeid annelids. In the artificial nest they accepted nearly every small arthropod offered them, including symphylans, diplopods (newly hatched and teneral), thysanurans, and entomobryid collembolans. Other species of *Strumigenys* and *Smithistruma* have been recorded with similarly broad diets (Wilson, 1954), but the general rule in the higher Dacetini, i.e. Orectognathiti, Epopostrumiti and Strumigeniti, is rather rigid specificity for collembolans. It is conceivable that acceptance of prey from among animal groups outside the Collembola was a reason why colony no. 610 was able to attain such extraordinary size.

Both in the field and in the artificial nests, the *Strumigenys loriae* were found to be the principal food gatherers. Hunting behavior in this species follows the pattern described by Brown and Wilson in previous papers as typical for the genus. On contacting prey, workers open their mandibles to more than 180°, turn quickly to face the prey head-on, and strike quickly and (usually) successfully. In our artificial nests, the workers were very efficient at finding and catching small animals placed within stalking range in the food chamber. Entomobryoid collembolans seemed to be the preferred prey for actual larval feeding.

Compared with the *Strumigenys*, the *Kyidris* workers were almost ineffectual as huntresses. They wandered through the food chambers of the artificial nests like any restless dacetines, but rarely attempted to catch, or succeeded in catching, prey. One was seen to seize a symphylan, pull it backwards, hold it for about thirty seconds without attempting to sting it, and finally release it when it began to struggle. Another seized an entomobryid, pulled it back vigorously, then lost it when the entomobryid kicked with its furcula. Another seized an entomobryid, successfully employed its sting, and was carrying it homeward slowly and awkwardly, when a *Strumigenys* worker came up and took the prey away. Still another *Kydris* was seen carrying an entomobryid at a brisk clip across the food chamber floor; it actually reached the entrance to the brood chamber before a *Strumigenys* met it and took its prey away.

The general impression was gained that predatory behavior has degenerated, but not completely disappeared, in the *Kyidris*. In the artificial nests, at least, the *Strumigenys* did the large part of the productive hunting. At the same time it must be recalled that at the nest site, only the *Kyidris* seemed to be associated with the coccids, although of course whether honeydew played any significant role in the colony's economy is completely unknown.

Brood Care and Adult Trophallaxis

Both species were solicitous toward the brood in colony no. 610, as shown by the readiness of both to move it when the brood chamber was exposed to light. There was no apparent prejudice on the part of either species for its own brood; each carried brood of either genus indiscriminantly and with equal care. As in the case of food gathering, however, the *Strumigenys* played the dominant role, and action on the part of the *Kyidris* tended to be infrequent and ineffectual. Both species were observed licking the brood. In one colony fragment containing brood of the *Strumigenys* only, the three *Kyidris* workers present spent much of their time licking the *Strumigenys* eggs, but despite close watching, we never saw a *Kyidris* do damage to an egg.

Adult trophallaxis was observed in the following combinations between the two species: *Strumigenys* donating to *Strumigenys*, *Strumigenys* donating to *Kyidris*, and *Kyidris* donating to *Kyidris*. It is possibly significant that there was no case recorded of the presumed parasite (*Kyidris*) donating to the host (*Strumigenys*). Moreover, in one instance recorded, a *Kyidris* worker interposed itself between two *Strumigenys* workers engaged in trophallaxis and began glossating the donor's mouthparts, whereupon the *Strumigenys* acceptor withdrew. On another occasion, a *Kyidris* worker diverted to itself for several minutes part of the ingluvium being passed from a *Strumigenys* worker to a *Strumigenys* dealate queen. This particular action, which might be termed "trophallactic theft", plus the fact that no *Kyidris* were seen donating to *Strumigenys* in trophallactic exchange, appear to us to be manifestations of a parasitic relationship, but not enough observations of this sort were made to settle the matter conclusively

Nest Building.

Soon after capture, a large section of colony no. 610 was placed in a a bottle with a quantity of nest material and the nest building activities subsequently watched. The *Strumigenys* workers were very active in this work, excavating incessantly over a period of several days, and piling heaps of loose wood and soil around multiple entrance holes. The *Kyidris* workers, on the other hand, were never observed to be engaged in nest building, but spent all of their time wandering restlessly through the galleries of the nest and over the nest surface.

Parabiosis or Primitive Social Parasitism ?

The relationship between *Strumigenys loriae* and the New Guinea *Kyidris* is of a kind which to our knowledge has never before been recorded in ants. In several ways it resembles parabiosis, as described by Forel

and other authorities in certain South American ants (cf. Wheeler, 1921). In these cases, two species belonging to different genera live in the same nest and use the same principal foraging trails. However, food gathering is carried on independently and the broods are kept strictly segregated. There occurs no contact between the two species that could be termed "social" in the strict sense. No interspecific trophallaxis is known to occur and most of the species have been found living independently as well as parabiotically.

The *Strumigenys-Kyidris* mixed colonies of New Guinea resemble the compound colonies of the South American parabionts in that they occupy the same nest. Moreover, food gathering is probably conducted in a more or less independent fashion, since each worker hunts by itself. But the *Strumigenys* and *Kyidris* go much further in the intimacy of their relationship. The brood of the two species is completely mixed, and is cared for, apparently without discrimination, by both species. Furthermore, there is free interspecific adult oral trophallaxis, at least from *Strumigenys*, as the donor, to *Kyidris* as the acceptor.

There is evidence that the *Kyidris* species are not independent of the *Strumigenys loriae*, as in the case of the parabionts, but that they actually live as obligatory parasites. This evidence can be summarized as follows.

1. No independent colonies of *Kyidris* were found in Papuasia. The four colonies of this genus discovered there were in each case mixed with *Strumigenys loriae*. On the other hand, independent colonies of *Strumigenys loriae* are abundant at the same localities and elsewhere.

2. The *Kyidris* workers, as compared with those of the associated *Strumigenys*, were almost ineffectual in hunting prey ; they were less active in moving brood when the nest was disturbed; and they did not participate at all in nest-building.

3. The intrusive method of solicitation practiced by the *Kyidris* on trophallactic pairs of *Strumigenys* is unusual among dacetines, and if it is a frequent occurrence, it would seem to indicate parasitic tendencies. Moreover, no instance of food donation by *Kyidris* to *Strumigenys* was observed, but as already noted, observations of trophallactic pairs were generally too few to make a point of this negative evidence.

4. The queens of *Kyidris yaleogyna*, and to a lesser extent those of *K. media* and *K. mutica*, show several modifications generally associated with parasitic habits in ants; these include a loss of pilosity, a smoothing of body sculpturing, a reduction in mandibular dentition, and possibly also the transparent film sometimes found on dealates.

5. Only *Kyidris* winged reproductives were present in the mixed colonies. This is, however, of limited significance, since winged reproductives were found in only a fraction of the "uninfested" *Strumigenys* nests during the same period.

6. Worker polymorphism of *Strumigenys loriae* was greatly reduced in the mixed colonies, the soldier caste being few in numbers or absent.

7. Limited introduction experiments carried on by Brown seemed to

show that *Kyidris yaleogyna* workers are much more conciliatory when introduced into strange *Strumigenys* nests than are workers of the non-parasitic dacetines *Strumigenys loriae* and *Smithistruma nigrescens*. Workers of the latter two species, when encountering workers of a strange species (such as *Strumigenys nidifex* of the Fijis) show immediate hostile behavior. A *Kyidris yaleogyna* worker introduced into a *nidifex* nest, on the other hand, made what appeared to be "supplicatory" motions, raising its head and antennae and lifting and moving its forelegs in a "pawing" movement. It made no aggressive moves on its own part, but was threatened and finally killed by the *nidifex* workers.

In our opinion the New Guinea *Kyidris* represent a very primitive level in the development of permanent, non-dulotic parasitism of the sort in which the host queen is preserved and the mixed colony can persist as such for an indefinite period of time. We would like to re-emphasize those features which we consider to be primitive in this respect: the parasite worker caste has undergone very little if any morphological change certainly identifiable with a parasitic mode of life; the parasite worker population is extraordinarily large in proportion to the host worker population; the parasite workers contribute something to the labor of the colony by hunting and brood-handling, although they show little efficiency in these tasks. We have no information as to how the parasitic queens found their colonies, but as mentioned previously, the morphology of the queens suggests intrusion into host colonies by means of conciliatory behavior. Moreover, the increment of both parasite and host queens in the mixed colonies may indicate that the *Strumigenys loriae* tend to be generally amicable toward alien queens of both the parasite and their own species.

Summary.

Two new species of the dacetine ant genus *Kyidris* from New Guinea are described. These were always found in mixed colonies with the larger, polymorphic dacetine species *Strumigenys loriae* Emery, which often occurs independently and is generally abundant in the lowland rain forests of New Guinea. The relationship of the *Kyidris* to the *Strumigenys* is interpreted as a very primitive level of permanent, obligatory, non-dulotic parasitism. Multiple queens of both genera occur together, and the brood is completely mixed. The worker population of the parasite is very large, and in one colony studied almost equaled that of the host. The parasite workers contribute to the colony labor by food-gathering and brood-handling, but are relatively inefficient in these tasks; they apparently do not participate in nest building at all.

Résumé.

Cet article décrit deux espèces nouvelles de *Kyidris* de la Nouvelle Guinée, genre de fourmis dacétines. Elles ont été trouvées toujours en colonies mixtes avec *Strumigenys loriae* Emery, grande dacétine polymorphe vivant souvent sans son parasite et commune partout dans les forêts humides tropicales à basse altitude de la Nouvelle Guinée. Les relations entre *Kyidris* et *Strumigenys* sont interprétées comme un stade primitif de parasitisme permanent, obligatoire et non-dulotique. De nombreuses reines des deux genres se trouvent ensemble dans le même nid, et leur couvain est complètement mélangé. Les ouvrières du parasite sont très nombreuses et, dans une des colonies étudiées, étaient presque aussi nombreuses que celles de l'hôte. Les ouvrières contribuent au travail de la colonie en recueillant de la nourriture et en soignant le couvain, mais d'une façon relativement inefficace; elles ne paraissent pas participer à la construction du nid.

(We wish to thank Prof. J. C. Bequaert for rendering the French translation of the summary and for other advice.)

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Figs. 1-5. — Females of the genus *Kyidris*. 1, *K. mutica* Brown, full-face view of head, Moriyama-mura, Tosa Prov., Shikoku, Japan. 2, *K. media sp. nov.*, full-face view of head, paratype. 3, *K. yaleogyna sp. nov.*, full-face view of head, paratype *ex* type nest. 4, Same, lateral view of body. 5, *K. media*, *sp. nov.*, right mandible of paratype. (Figs. 1-3 drawn to the same scale.)

OBSERVATIONS ON MACROTERMES GILVUS HOLMGR. IN JAVA-3 ACCUMULATIONS OF FINELY CUT VEGETABLE MATTER IN THE NESTS (*)

by

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Oscar John has recorded (1925:375)** that among the many *gilvus* nests which he examined during his four months'explorations in Malaya and Sumatra in 1913, only one contained piles fofo comminuted wood ('Anhäufungen von zerkleinerten Holzes').

Bathellier (1927), however, repeatedly mentions the frequent occurrence of finely cut particles of wood and other organic material accumulated in chambers in the basal part of *gilvus* mounds in Indochina. He describes them in one place as 'débris ligneux d'environ un millimètre taillés et accumulés par les termites' (p. 193), in another place as 'fragments de graminées que les termites emmagasinent' (p. 195) and finally as 'une couche de petits fragments végétaux, disposés exactement comme le serait une meule sur une surface identique' (p. 199). Also, the same author examined the individual particles of the deposits with a lens and found 1) small pieces of grass staks, 1.3 mm long and 1 mm thick, and 2) fragments of leaves of about the same size, part of which could be recognized as having been cut from grass blades and from dry fallen mango leaves. Mango trees were present in the vicinity of the nest (p. 200).

In the descriptions of *gilvus* nests by Kemner (1934) only one passage dealing with this topic can be found. Here he records (p. 188) that one cavity in a young nest at Bogor (W. Java) probably functioned as a storeroom, because the upper part contained fungus combs while the galleries in the lower part were wholly filled with finely cut vegetable matter.

The present author briefly commented on his discovery of stores of chopped leaves and stalks, during a communication about his investigations combs.

(*) Elaboration of part of the paper read at the 2nd Congress of the U.I.E.I.S. held at Würzburg in April 1955.

(**) For the literature references see first contribution (p. 321 of volume II of *Insectes Sociaux*, 1955).

The piles of fragments have been found in different circumstances, places and seasons. They are to be met with only when one digs deep into the mound and this may be the reason why they have seldom been observed or even been wholly overlooked by workers in the field like JOHN, KEMNER and UICHANCO. Moreover, they appear to occur in very different quantities, even in nests of the same locality and at the same time of the year. Sometimes only a few teaspoonfuls can be gathered, in other instances there will be enough to fill a few dessert-spoons. In one nest part of the smaller tunnels were found to be filled up entirely with the material. But more often they appeared to be absent.

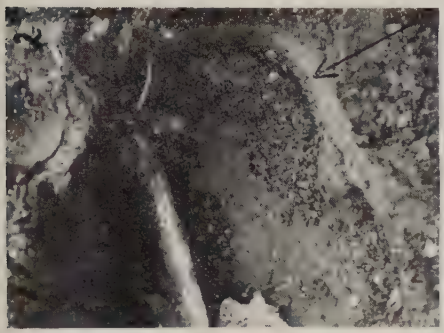
Most of the investigations in the *gilvus* mounds happened to be carried out in May-June of 1935 and 1936 (that is in the first months of the dry season) and in January-February 1936 (in the midst of the wet season) in localities near the field station of Gedangan in C. Java and in the plain of Indramayu in W. Java, and in several nests the stocks of fragments were observed. Incidentally the presence of "wood-crumbs" was observed in a nest situated in the teak forest of C. Java in the month of August (in the height of the dry season). However, during a very thorough investigation of a mound in the month of October (end of dry season) (as described in Entom. Ber. Ned. Ind. 7, 1941, p. 30) no piles of fragments were seen. Judging from the field notes the accumulations were encountered in nests with thriving populations engaged in the building of new combs. From this it should not be concluded, however, that the stocks are always present in such nests. Further observations are much needed to establish any such correlation.

In one nest the piles of fragments looked stale and mouldy, the crumbs were somewhat stuck together, and a Myriapod (Geophilid) was found on them, all very abnormal features. Now it looked as if this nest (figured in this volume on Planche fig. 3, p. 457) had either been through a bad period or that the colony had re-occupied a deserted mound.

Composition of the heaps. In order to have the components of the sawdust piles properly identified, some eight samples were submitted for examination to Miss Dr B. POLAK, then botanist on the staff of the Soil Research Institute at Bogor. The results of the examination were laid

DESCRIPTION OF FIGURSE IN PLATE. Accumulations of finely cut matter in cavities of *Macrotermes gilvus* nests (see black arrows).

1. Cavity exposed on vertical cut through a mound in W. Java, Jan. 1936. It contains remaining parts of fungus combs supported by a clay structure. The accumulation is on the bottom. 2. Ditto. Cavity nearly empty, crossed by a living root. A substantial deposit at the right. 2a. A part of the same enlarged. 3. Longitudinal room uncovered after lifting a root of a dead stub which enveloped a mound. Photograph from above. An oval pile next to the white, worn comb. Teakforest in C. Java, May 1936. 4. Marginal basal part of nest exposed after lifting a big which covered a mound. Thin layers of the finely cut matter in the roomy galleries. At the right a fresh comb in a cavity. Teakforest in C. Java, May 1936.











down in a short report dated 16-7-1942. This was received during the Japanese occupation and no further discussion or elucidation of the matter was possible at the time. These were Miss Polak's findings:

Sample 1 (4.0 grm): mainly particles of wood, a few fragments of bark, small black globules (excreta ?), fragments of chitinous skeleton.

Sample 2 (7.9 grm): mainly fragments of Graminaceae, bits of leaves of Dicotyledons, animal hairs ?, fungi and fungous spores, Arcella, soil particles.

Sample 3 (7.2 grm): mainly fragments of leaves of Dicotyledons, pieces of Graminaceae and Cyperacease, particles of dicotyledonous stems, chiti-

into the interior of *gilvus* nests in Mid Java, at a meeting in Bogor. On that occasion he also showed a few photographs to illustrate this point. (Entomologische Meded. v. Ned. Indië, 2, 1936, p. 3).

The Philippine authors Uichanco (1919) and Panga (1936) do not mention the heaps of vegetable fragments in their descriptions of *gilvus* mounds.

Many interesting details have been revealed by Grassé about the occurrence of piles of sawdust-like matter —'boules de sciure' or 'amas de sciure' — discovered by him during his investigations into nests of *Bellicositermes natalensis* in equatorial Africa (1937). Further particulars, amplified with observations on similar deposits in nests of *Acanthotermes acanthothorax* and *Pseudacanthotermes spinifex*, were given in the account of later investigations by Grassé and Noirot (1944-1945).

Most observations were made by the French authors on the 'sawdust piles' in *natalensis* mounds. They are composed of vegetable fragments of widely different kinds, such as minute thorns, bits of grass, pieces of leaves, fragments of fruit husks, dry calyces, twiglets, mixed with occasional grains of sand, bits of gum, etc., all gathered by the worker termites from the soil surface outside the nests at dusk or during the night. The fragments are collected into cavities in the upper part of the habitaculum, where they are piled into heaps sometimes bigger than a fist. A very important detail is that the material is soaked in a liquid rich in bacteria, probably saliva, to such an extent that the liquid comes out easily when the material is squeezed between the fingers. After the piles have dried somewhat and have become fairly solid, they are excavated by the termites, which gives them the appearance of fungus combs. No fungi grow on them, however, but numerous maggots and Collembola may be present in them and on their surface.

In *Pseudacanthotermes* the fragments are spread in thick layers around the fungus combs or even beneath them, in *Acanthotermes* the piles are shaped into small balls or 'olives' of some 2 cm in diameter.

Hitherto unpublished information about the occurrence of piles of vegetable fragments in the *gilvus* nests in Java is now presented.

Location and quantity. The accumulations have been found exclusively in the lowest parts of the nests. Here they are spread in layers on the floor of wide galleries or tunnels leading from the surrounding soil to the

nest proper, and on the floor of the irregular cavities which are typical of the deepest part of the habitaculum or 'hive'. These cavities may be otherwise empty, or they may contain remnants of used fungus combs still supported by a delicate structure of clay pillars (fig. 1). In a few cases the fragments were found lying right under still solid combs. The accumulations look like heaps of crumbs, dark in colour and moist; not seldom a few green fragments are seen among them. One field note mentions that they have a musty odour, but under normal conditions they are never spun over with fungal hyphae, as happens on the surface of fresh nous skeleton, insect head, Arcella, soil particles.

Sample 4 (1.2 grm): parts of leaves and stalks of grasses and Cyperaceae, utriculi of Carex, Rhizopod houses (thecae), fungi.

Sample 5 (1.2 grm): fragments of leaves of Dicotylodons, pieces of leaves and stalks of grasses and Cyperaceae.

Sample 6 (0.2 grm): mainly fragments of leaves of Dicotyledons, particles of wood, bits of grass cuticle, single vascular bundles, fungi, soil particles.

Sample 7 (0.1 grm): mainly fragments of leaves and stems of Dicotyledons, a few pieces of grass cuticle, single vascular bundles, fungi.

Sample 8 (Collected from nest in golf links near Bogor): mainly fragments of grass blades, husks fofo Graminaceae, small flower bud, rootlets; fragments of Cyperaceae leaves, rootlets of Cyperaceae; fragments of smooth-margined leaves of a Dicotyledon (rather abundant); fungi.

Size of crumbs.

Sample.	2-1 mm	1-0.5 mm	0.5-0.2 mm	0.2-0.1 mm	0.1-0.05 mm	
1	0.600 36.5 %	0.465 28 %	0.365 22 %	0.040 2.5 %	0.170 10.5 %	= 1.640 grm
2	1.283 58 %	0.710 32 %	0.185 8.5 %	0.010 0.05 %	0.015 0.1 %	= 2.203 grm
3	1.880 58 %	1.010 31 %	0.303 9.5 %	0.025 0.8 %	0.030 0.9 %	= 3.248 grm
4	0.218 25 %	0.360 41.5 %	0.230 26.5 %	0.020 2 %	0.040 4.5 %	= 0.868 grm
5	0.182 21 %	0.540 62 %	0.125 14 %	0.010 1 %	0:015 1.5 %	= 0.872 grm
6	0.020 21 %	0.044 41 %	0.015 16 %	0.010 10.5 %	0.006 6 %	= 0.095 grm
7	0.020 28 %	0.030 42.5 %	0.010 14 %	0.005 7 %	0.005 7 %	= 0.070 grm
8	0.019 17 %	0.058 52 %	0.018 16 %	0.007 6 %	0.010 9 %	= 0.112 grm
	4.222 46 %	3.217 35 %	1.251 14 %	0.127 1.5 %	0.291 3.0 %	= 9.108 grm

In addition to Miss POLAK's identifications it may be said that a large part of the fragments of leaves present in the piles of nests in teak forests were recognized by the author, from their nervature, as originating from teak leaves (Tectona grandis). The green fragments mentioned in the former paragraph looked like small lengths of grass stalks.

Accompanying the list of components was a table giving figures on the size-frequency of the fragments in parts of the samples. The figures had been computed, apparently, following a standard method of sieving by an assistant. The table is reproduced here for the final figures only and with the sum total and percentages added.

The proportional compositions show some differences for the various samples but it is quite clear that crumbs of ½-2 mm constitute the main part—some 80 %— of the material. The quantities in the 0.05-0.1 mm size-grade are very small and may have been composed of dust formed during the drying, handling and sieving of the samples, in which brittle fragments of leaves constituted such a large part.

From the combined data it appears that the accumulations of finely cut material are composed mainly of fragments of plant parts of various origins, most of them from leaves and stalks. Comminuted wood is present only in two instances. Fragments of grasses and Cyperaceae are rather numerous. The occasional particles of non-vegetable origin, as those of animal matter and soil particles, should perhaps be looked upon as incidental admixtures.

Method of collection of the fragments by the termites In 1938 Ir LEVERT manager of the big Cocoa and Kapok Estate Siluwuk Sawangan (near Weleri in C. Java) told my colleague C. J. H. Franssen of a most interesting observation he had made. Ir LEVERT had seen multitudes of termites—apparently the common big rayap—*Macrotermes gilvus*— coming out of the soil at night and feeding on dry cocoa leaves on the ground. The activity of the termites had been detected through a rustling noise made by the insects, which resembled light rain. The phenomenon had repeatedly been observed and could be shown to Dr FRANSSEN during his visit.

The present author had never seen anything of the sort nor had his Javanese assistants of the field laboratory at Gedangan in the middle of teak forests, although our investigations into the swarming habits of the teak trunk termite (*Neotermes tectonae*) had taken us all more than once into the forest after dusk.

The observation, however, was confirmed by the well-known and able part-time entomologist Dr E. JACOBSON, who had witnessed the appearance of *gilvus* termites in his own garden at Tjandi-Semarang (C. Java) at the time. The rustling noise was heard particularly when the termites had been disturbed by a light thrown on them.

The noise might well have been produced, in the author's opinion, by the soldier termites rapping their heads against the substrate, as has been noticed in other termite species when colonies are disturbed.

With regard to the green particles found in the accumulations and evidently cut from still living tissues, another observation may be related here. Once, while watching the swarming of *gilvus* alates from a subterranean nest in a garden in Bogor, the author was struck by the fact that some of the numerous workers, flocking out as usual in such occasions from the temporary openings, took to biting small circular pieces from the margins of blades of grass (the grass species involved was "djukut pahit", possibly Anastrophus compressus). (**).

This may be the right place to mention still another experience about *gilvus* termites cutting grass. In 1937 serious damage was reported to the grass cover of greens on the golf links at Tegal Sapi near Bogor. The greens were planted with a fine species of grass, said to have been specially imported from Singapore for the purpose a year and a half before. (The grass was afterwards identified by Dr Van Steenis of Bogor Herbarium as Digitalis longiflora, a common species all over Java.) Repeatedly parts of the turf became withered and it appeared that in those places the grass had been bitten through near the surface and severed from the roots. It could be picked up in tufts. It was established that this was due to the activity of *gilvus* termites, whose presence was otherwise not particularly noticeable there. The links were laid out on hill slopes entirely covered with grass with a few scattered woody shrubs of Melastoma, Lantana, Stachytarpheta, etc.

Conclusion.

These observations on the piles of finely cut vegetable matter in the Javanese *gilvus* nests agree very well with those made by Bathellier in Indochina, and besides, provide some useful additions to them. In many points they are also in agreement with the observations of Grassé et Noirot for the African species. The main differences with the habits of *natalensis* in this respect appear to be that in the latter species the particles are piled up in the uppermotsts part of the habitaculum and are made into rather firm lumps, which are excavated afterwards. Therefore, the method of storing of *gilvus* seems to bear a closer resemblance to that of *Pseudacanthothermes*.

With regard to the function of the collection and storage of the vegetable fragments in the complex food-economy of the termites, the author's observations allow of no definite conclusion. There can be little doubt, however, that the piles must be looked upon as part of the preparations for the building of fungus combs. This supposition has gained a good deal more probability since Grassé et Noirot found that a small "amas de sciure de bois" appeared in newly founded colonies of *natalensis* just before the first minute "meule à champignons" was constructed (*Insectes Sociaux* II, 3, 1955: p. 215).

(**) A brief account of these observations was given at a meeting of the Nederlandsch Indische Entomologische Vereeniging, held at Bogor on 12 October 1938 (see Entom. Med. v. Ned.-Ind. 4 [1939], p. 35).

II

NOUVELLES DE L'UNION

TRAVAUX PUBLIÉS PAR DES MEMBRES DE L'UNION

Abbott (C. P.), Butler (C. G.). — 1952. **The scientist and the cine-camera.** (*Rep. Cent. Ass. Beekeep., Oct.*)

The use and value of the cine camera as a tool in bee research, particularly with respect to investigations on bee behaviour, are discussed.

Bailey (L.). — 1952. **The action of the proventriculus of the worker honeybee** *Apis mellifera* L. (*J. exp. Biol.*, **29**, 310.)

A detailed account is given of the method of filtration of small particles (pollen grains and Nosema spores) by the proventriculus from the honeystomach. The rates of filtration of different concentrations and sizes of particles, and of different volumes of suspensions, are analysed and the possible physiological significance of the filtration activity is discussed.

Bailey (L.). — 1953. **The effect of fumagillin upon** *Nosema apis* (Zander). (*Nature, Lond.*, **171**, 212.)

The curative effect of fumagillin upon an established infection within individual bees is described. The drug acts upon the developing intracellular stage of the parasite, but relapses occur even after continuous treatment for seventeen days.

Bailey (L.). — 1953. **The treatment of Nosema disease with fumagillin.** (*Bee World*, **34**, 136.)

The results of autumn treatment of infected colonies with fumagillin are given. The preventive effect of this treatment upon the resurgence of the disease during the following spring was striking. However, a low level of infection became apparent in treated colonies in late spring. It is considered to have arisen from the old comb, which still contained viable spores from the previous year.

Bailey (L.). — 1953. **The transmission of Nosema disease.** (*Bee World*, **34**, 171.)

The carrying over of the disease from one year to the next by spores upon comb has been demonstrated. The transference of colonies from old combs to new comb foundation during early summer has been shown to be effective in breaking the cycle of infection, as the transmission of this disease from infected to healthy bees virtually ceases during the flying season.

Bailey (L.). — 1954. **Nosema disease.** (*Bee World*, **35**, 69.)

Bailey (L.). — 1954. **Bee Poisoning.** (*Bee World*, **35**, 221.)

Bailey (L.). — 1954. **The control of Nosema disease.** (*Bee World*, **35**, 111.)

The results of final experiments on the effect of transferring colonies on to clean comb are given. The disease was eliminated when bees were transferred on to clean comb and were allowed to recover their brood and stores from the old comb before the latter was removed. Methods and results of sterilizing old comb with acetic acid and formalin are given.

Bailey (L.). — 1954. **The filtration of particles by the proventriculi of various aculeate Hymenoptera.** (*Proc. Roy. ent. Soc.*, **29**, 119.)

The correlation between the anatomy of the proventriculi of various hymenoptera and their efficiency in filtering particles from liquid suspension in the crop is described. The physiological significance of this function is discussed.

Bailey (L.). — 1954. **The respiratory currents in the tracheal system of the adult honeybee.** (*J. exp. Biol.*, **31**, 589.)

The inactive bee inhales and exhales via the first thoracic spiracle. In air containing a high concentration of CO_2 the propodeal spiracle becomes inactive and its opening movements are synchronous with abdominal pumping. Under these conditions there is a marked current of air through the thorax, entering via the first thoracic spiracle and leaving via the propodeal spiracle.

Blackith (R. E.). — 1900. — **The Analysis of Social Facilitation at the Nest Entrances of some Hymenoptera.**

The passage of unmarked social hymenoptera in and out of their nests is decisively non-random, grouping being demonstrated with both wasps and bumble bees. The observed distributions follow the negative binomial, one plausible interpretation of which assumes that workers are inhibited from passing through the nest entrance until sufficient individuals have accumulated to act as a releaser. Most workers of the red wasp *Vespula rufa* are released by the accumulation of from one to three further workers at the entrance. Other species of wasp seem to have less marked inhibitions. Young queen bumble-bees (*Bombus lapidarius*) have significantly higher inhibitions than have workers of this species. Worker wasps may obtain their releaser from individuals passing in the opposite direction only when insufficient pass in the same direction.

Different types of test reveal non-random passage of the nest entrance when many or when fewer insects are active. Grouping may be measured by the entropy of social organization. Somes methods of estimating the number of workers foraging and of the mean duration of a flight, depend on a complete return of workers to the nest at night. A dawn to dusk record shows that this return may be far from complete, leading to biassed estimates.

Brian (M. V.). — 1955. **Food collection by a Scottish Ant Community.** (*J. Anim. Ecol.*, **24**, 336-51.)

1. The feeding system of a four-species community of rather primitive ants characteristic of west Scotland, has been studied. The species were *Formica fusca* L. *Myrmica rubra* L., *M. scabrinodis Nyl.* and *Leptothorax acervorum* Fab.—2. Small sources of sugar could be monopolized, especially if near to the nest, and actual occupation by a group of workers was the main essential to this, although the largest species, fusca, could sometimes dislodge the others. The ability to find a source and mobilize feeders on it was a greater guarantee of success than ability in fighting.—3. The hunting, distribution of rubra was asymmetrical about the nest, even in isolated colonies. In dense groups of colonies, nesting in rotting tree stumps and foraging into long herbs, the same individual asymmetry existed with a tendency for these areas to fit together so that the whole area was searched. These rubra home-ranges were entirely overlapped by the much larger ranges of fusca and acervorum.—4. Three of the species were shown to vary in their propensity to ascend vegetation. *Myrmica scabrinodis*

foraged principally on the soil surface and perhaps below, fusca readily climbed vegetation, whilst rubra was intermediate in this respect.

Brian (M. V.), Brian (A. D.). — 1955. **On the two forms Macrogyna and Microgyna of the ant *Myrmica Rubra* L.** (*Evolution*, No. **3**, 1955.)

The degree of reproductive contact between the populations of two integrading forms of *Myrmica rubra* L. (now designated as the sub-species macrogyna and microgyna) is considered. Like matings are more frequent than unlike, but not good evidence of selection by the individuals concerned could be obtained. Rather it appears to be due to circumstances created by differences in the space-time distribution of the populations. Such differences arise directly and indirectly from the reproductive differences between the subspecies which adapt them severally to seral (macrogyna) and biotic plagioclimax (microgyna) vegetation respectively. Such intermediates (assumed to be hybrids) as occur are likely to be sub-viable for socio-ecological reasons (although physiological and genetic ones may reinforce these). It is suggested that evolution from a less specialised form must have occurred during spatial isolation under different ecological conditions.

Butler (C. G.). — 1939. **The drifting of drones.** (*Bee World*, **20**, 140-42.)

Large numbers of drones belonging to several different colonies were marked with coloured paints, each colony being given its own distinguishing mark. Subsequent observation of the distribution of these drones in the apiary, which contained some 20 mating nuclei as well as 40 full-strength colonies of bees, led to the conclusion that drones seldom drift from their own hive into that belonging to another colony or even into a nucleus with a virgin queen. Drones will, however, join any swarms which happen to be about, being readily accepted and, having once joined them, remain attached to them thereafter.

Butler (C. G.). — 1939. **An automatic drinking fountain in the apiary.** (*Bee World*, **22**, 119-120.)

A well-protected, warm and easily cleaned drinking foutain with automatic control of the water supply by means of the float-chamber of a carburetter is described.

Butler (C. G.). — 1940. **The choice of drinking water by the honeybee.** (*J. Exp. Biol.*, **17**, 253-261.)

The honeybee prefers dilute sodium chloride and ammonium chloride solutions to distilled water. She does not prefer concentrations of these salts higher than N/20 solutions, and solutions of various other salts to distilled water. The honeybee appears unable to distinguish between N/160 sodium chloride or N/160 ammonium chloride and distilled water. Bees are probably largely attracted to such sources of drinking water as rain water gutters choked with decaying organic matter, swetage effluent, etc., by a water perception sense coupled with an olfactory appreciation of various volatile substances contained in these sources of water.

Butler (C. G.). — 1940. **The ages of the bees in a swarm.** (*Bee World*, **21**, 9-10.)

As a result of marking experiments and the subsequent analysis of bees in prime swarms into age groups it is concluded that a swarm is largely composed not of the older bees, as had previously been assumed, but of the younger and middle-aged bees.

Butler (C. G.). — 1941. **A possible new cure for acarine disease of honeybees.** (*Nature*, **148**, 86.)

The vapour of terpineol, a heavy fraction of crude pine oil, was found to be highly toxic to the nymphs and adults of *Acarapis woodi* but to be harmless to adult bees and their brood.

BUTLER (C. G.). — 1941. **A study of the frequency with which honeybees visit red clover (*Trifolium pratense*) together with an examination of the environmental conditions.** (*Ann. Appl. Biol.*, **28**, 125-134.)

Honeybees were found to work red clover, both first and second crops for pollen and nectar. Two peak periods of activity, about 10.30 a.m. and 3 p.m. (G. M. T.) are exhibited by pollen gatherers: it is probable that these plants reach their peak of pollen dehiscence at these times. The visits of honeybees to collect nectar are chiefly determined by the height reached by the nectar in the corolla tubes of the flowers. When the sugar concentration of the nectar of red clover flowers was lower than that of other "honey" plants in bloom at the same time in the locality, or when the nectar was not sufficiently high in the corolla tubes for easy collection, bumblebees were usually more abundant on red clover than honeybees, except at the peak periods of pollen collection. When conditions were suitable for the nectar collection five or six times as many honeybees as bumblebees were usually present. Few insects other than honeybees and bumblebees were found working red clover.

The honeybee carries on an average about 284,000 red clover pollen grains per load and visits a minimum of 284 flowers in collecting this load. In the U. S. A. honeybees have been credited with the cross-pollination of about 82 per cent of the red clover crop, bumblebees with 15 per cent, and the hymenopterous, lepidopterous and dipterous pollinating insects with 3 per cent. No comparable data collected in this country are available for cross pollination of an important part of the seed crop.

BUTLER (C. G.). — 1943. **Bee paralysis, May sickness, etc.** (*Bee World*, **24**, 3-7.)

There are a number of complaints and one true disease of the honeybee which all exhibit very similar signs in the apiary, and which may conveniently be grouped together as Bee Paralysis. Nine types of Paralysis are distinguished, most of them being due to a dietary upset or poisoning. Paralysis due to the consumption of frost-damaged pollen, honeydew from lime trees, concentrated lime nectar, the spores of the fungi *Aspergillus calyptratus* and *A. versicolor*, etc., is described. It is pointed out that these forms of paralysis, although sometimes serious in their effects, soon disappear once the causative agent has been removed, which fact accounts for the sudden ontset and equally sudden disappearance of the complaints in the apiary.

BUTLER (C. G.). — 1943. **The position of the honeybee in the national economy.** (*Ann. Appl. Biol.*, **30**, 189-191.)

The main function of beekeeping in both peace and wartime is the provision of pollinators for fruit and seed crops. There is good evidence that in many places where large orchards or large areas of insect-pollinated seed crops are planted, there are insufficient wild pollinating insects present for full production to be obtained. Man has upset the balance between the numbers of flowers requiring pollination and the number of pollinating insects available to effect their pollination. The honeybee is the only pollinating insect which can readily be used to redress the balance. It has been estimated that the average annual value of each colony of bees to the nation is about £ 12.

BUTLER (C. G.). — 1943. **Work on bee repellants. Management of colonies for pollination.** (*Ann. Appl. Biol.*, **30**, 195-196.)

It was found that lime sulphur, nicotine and nicotine sulphate were all capable when added to spray mixtures containing arsenic of repelling honeybees from collecting these mixtures as drinking water. If applied to open flowers, they had some, but not a 100 per cent, deterrent effect upon honeybees attempting to visit these blossoms.

BUTLER (C. G.). — 1945. **The incidence and distribution of some diseases of the adult honeybee.** (*Ann. Appl. Biol.*, **32**, 344-351.)

Since 1918 four complaints of the adult honeybee, acarine disease, nosema disease, amoeba disease and bee paralysis, have been recognised in this country. Surveys

designed to discover the incidence and distribution of these diseases were carried out during the winter 1941-1942 and 1943-1944. It was found that none of these diseases is clearly confined to any definite areas of England and Wales. Acarine disease, however, is apparently more abundant in the west and south-west; and nosema disease appears to be most prevalent in the home counties and also has other areas of heavy infection in Leicestershire and Cumberland, Lancashire and Yorkshire. Bee paralysis in its various forms is both widespread and common, and amoeba disease, although relatively rare, has been found to be widely distributed throughout the country.

Butler (C. G.). — 1945. **The behaviour of bees when foraging.** (*J. Roy. Soc. Arts*, **93**, 501-511.)

From the 20th day of adult life onwards the young worker honeybee is concerned with the collection of water, pollen and nectar. She finds her way back to her hive from a foraging site by means of at least three senses, a sense of direction, a sense of distance travelled and also a sense which enables her to locate visual landmarks near her hive and to orientate herself correctly thereto. Bees do not wander at random over any given crop but confine their attention to a small area of the crop. These "fixation areas" of individual bees overlap to some extend and thus some cross-pollination is effected. It is nevertheless difficult to see at first sight how cross-pollination is effected in an orchard, as we know it is, where a single tree or even a part of a tree may serve as the "fixation area" of an individual bee. It has been found, however, that if the population of pollinating insects, and therefore the degree of competition, is sufficiently great, then there is a "wandering" population of bees seeking "fixation areas" of their own, superimposed upon the "fixed" population. It is this "wandering" population, which is mainly composed of young bees, which provides the cross-pollinators. It is now considered to be best for fruit growers to place colonies of bees, maintained in their orchards for purposes of pollination, together in one or more groups somewhere near the centre of each 30 acres of orchard, irrespective of the number of colonies available, rather than to scatter them about throughout the orchard. If this is done the grower can, over several years, find out the necessary number of colonies of bees of any given strength required if full production is to be obtained. Seed growers, whose problems are different, can none-the-less also use honeybees to advantage in many districts and also determine how many colonies of bees they will require.

Butler (C. G.). — 1945. **The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and nectar concentration and abundance.** (*J. Exp. Biol.*, **21**, 5-12.)

Both nectar abundance and concentration appear to have considerable effect upon honeybee activity. From the data at present available, it appears reasonable to conclude tentatively that nectar concentration decides in the first instance which species of plants will be visited in preference to others in flower at the same time, and that nectar abundance then determines the proportion of the foraging population of a colony which will work the flowers in question.

Butler (C. G.), Cockbill (G. F.). — 1942. **Preliminary investigations on the value of electric heating of beehives.** (*Ann. Appl. Biol.*, **29**, 34-42.)

The general effect of all intensities of heating appeared in these experiments to be to reduce the area of brood present in mid April and to increase the winter consumption of stores, in direct contradiction to any belief in a beneficial effect on the colony.

Butler (C. G.), Finney (D. J.). — 1942. **The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and solar radiation.** (*J. Exp. Biol.*, **18**, 206-212.)

A review of the literature shows that those who have studied the influence of solar radiation on honeybee activity are agreed that it is an important limiting factor. Fresh analysis of some of this data, however, throws doubt upon some of the conclusions

previously reached. New data were, therefore, collected which clearly show an association between variations in honeybee activity and the radiation of clear light.

Butler (C. G.), Finney (D. J.), Schiele (P.). — 1943. **Experiments on the poisoning of honeybees by insecticidal and fungicidal sprays used in orchards.** (*Ann. Appl. Biol.*, **30**, 143-150.)

Of the common constituents of spray mixtures only lead or calcium arsenate were found to be likely to cause serious honeybee poisoning, though Derris emulsion may cause slight poisoning. Lime sulphur, nicotine sulphate and copper sulphate are all repellent to bees. Concentrations of 1/500 lime sulphur or 1/2000 nicotine sulphate were sufficient to reduce the uptake of M/1 sucrose to less than 10 per cent. of that of unadulterated sucrose solutions. The presence of lead arsenate in these solutions appeared to make them even more repellent. Lead arsenate solutions were found to be no more attractive to bees than distilled water. Bees may collect arsenic when visiting fruit trees, or plants growing beneath or near the trees, for pollen and water, contamined water apparently being the chief cause of poisoning. The addition of 1 per cent. lime sulphur was sufficiently deterrent to prevent bees collecting contaminated water. The other cause of arsenic poisoning is the collection by the bees of contaminated pollen and can be most serious. This form of poisoning can only be prevented by growers refraining from spraying open blossom.

Butler (C. G.), Jeffree (E. P.), Kalmus (H.). — 1943. **The behaviour of a population of honeybees on an artificial and on a natural crop.** (*J. Exp. Biol.*, **20**, 65-73.)

In an experimental field filled with dishes of syrup to represent flowers individual bees were observed to visit one chosen dish with great regularity provided that the supply of syrup did not become exhausted. Bees were deterred from collecting syrup from dishes placed even partially in shade and they very seldom worked beneath the shade of trees. Over the range of distances covered (160-400 yards) they were always more visitors to the nearer than to the more distant dishes; the extent of the difference, however, varied from day to day. Bees accustomed to collect syrup from the dishes furthest from the hive did not move to sites nearer home when the weather became unfavourable. There was some evidence, however, that bees working a long way from the hive were more easily deterred from foraging by unfavourable weather than those working close to the apiary. Bees marked on a patch of *Epilobium augustifolium* situated in the midst of a fairly large crop of this plant, were usually recovered within 5 yards of the point of marking. Such bees remained "fixed" to his area for days. The same was found to be true with other plants.

Butler (C. G.). — 1946. **The provision of supplementary food to hive bees.** (*Ann. Appl. Biol.*, **33**, 307-309.)

Four British Standard brood combs full of pollen provide the necessary protein requirements for a colony on B. S. equipment from late autumn until April of the following year.

Sucrose syrup is not so satisfactory as honey as winter and spring food for bees, but a mixture of equal parts of honey and syrup proves to be satisfactory. The strongest colonies in April are produced by confining feeding to autumn, and wintering the bees on 35-40 lb. of honey or honey and concentrated sucrose syrup. Feeding with syrup and pollen is only found to be advantageous when the colony concerned lacks adequate reserves of carbohydrate and protein; the feeding of honey or syrup in spring may have a retarding rather than a stimulative effect upon colony development.

Butler (C. G.). — 1946. **Further investigations on the value of electric heating of beehives.** (*Ann. Appl. Biol.*, **33**, 310-313.)

Three groups of colonies of bees were employed, two of these groups having heat applied to them by means of a specially designed frame heater, different intensities of heat being applied in each case. No noticeable effect on the consumption of stores

was observed, and the heated colonies were weaker than the unheated colonies at the beginning of May. Colonies in top entrance hives wintered no better than those housed in normal bottom entrance hives, nor were significant differences in brood chamber temperatures recorded.

It is concluded that no benefit was obtained from electrical heating at the intensities of heat applied.

Butler (C. G.). — 1946. **Bee culture in the U. S. A.** (*Agriculture*, **53**, 265-268.)

A report on a tour of bee Research Centres and Agricultural Research Stations, etc., in the U. S. A.

Butler (C. G.). — 1946. **Bee culture and research in the U. S. A.** (*Ann. Rept. Central Assoc. of B. B. K. A.*, 2-10.)

A brief report on a visit made to North America and of bee research work in progress in the Federal and some State laboratories. Particular reference is paid to work on artificial insemination of queen honeybees; the resistance of certain strains of bees to American Foul Brood : European Foul Brood: the sulphonamide treatment of American Foul Brood.

Butler (C. G.). — 1947. **Some trends of bee research to-day.** (*J. Dept. Agric. Scot.*)

Butler (C. G.). — 1948. **Aspects of Bee Behaviour.** (*Discovery*, 9, 107-110.)

A short, popular account of some recent research on the foraging behaviour of honeybees and of the methods of communication practised by them.

Butler (C. G.). — 1948. **Bee Research.** (*Scottish Agriculture*, **27**, 131-135.)

An account of the development of the technique of artificial insemination of queen honeybees and of the part which this new technique is likely to play in the development of strains of bees for the pollination of the flowers of specific seed crops. The control of American Foul Brood by the development of strains of bees that exhibit resistance to the disease, and by the use of sulphonamides, etc., is also discussed.

Butler (C. G.). — 1948. **Bee Behaviour.** (*Nature*, **163**, 120.)

A condensed discourse on recent work on the division of labour in the honeybee colony and of the behaviour of honeybees in the field whilst seeking nectar and pollen.

Butler (C. G.). — 1949. **An Introduction to the Sense Physiology and Behaviour of the Honeybee.** (*Book. Oxford Univ. Press.*)

Butler (C. G.). — 1949. **Some trends in bee research today.** (*Ann. Rpt. Central Assoc. of B. B. K. A.*)

Butler (C. G.). — 1950. **A new design of microsyringe tip for instrumental insemination of queen honeybees.** (*Nature*, **166**, 957-958.)

A description of a syringe tip which enables the syringe to be held in the hand throughout the operation of introducing semen into the queen honeybee, and allows of easy introduction of the syringe without the use of a probe.

Butler (C. G.). — 1951. **The importance of perfume in the discovery of food by the worker honeybee** (*Apis mellifera*, L.) (*Proc. roy. Soc. B.*, **138**, 403-413.)

Worker honeybees have an inherent tendency to associate certain perfumes with food. This results in untrained scouting bees being attracted to certain kinds of flowers, such as hawthorn and wild white clover, which they have never visited before.

If the perfume of a crop of newly-opened flowers is sufficiently powerful, it sometimes attracts scouting bees from a considerable distance away. But, normally, a bee has to approach to within a few centimetres of a mouth of a flower before she can appreciate its perfume. If a bee has learned to associate a particular perfume with a particular

group of flowers she will seldom enter any flower in the group unless she can smell its perfume.

When a bee is attracted towards a flower or flower-like object and approaches it closely, any attractive perfume it may possess tends to acts as a stimulus to further exploration which may involve settling on the object and possibly extending her tongue and seeking food in any small crevice in or around the object.

In general, the results obtained with untrained bees support the conclusions reached by von Frisch in 1919 in his work with trained bees, and suggest that both of these categories of bees behave in a similar way when seeking food.

Butler (C. G.). — 1951. **Beekeeping and agriculture.** (*Brit. agric. Bull.*, **4**, 16.)

A discussion of the part played by honeybees in the pollination of fruit and seed crops, and of the way in which recent advances in bee research have made it possible for beekeepers to co-operate with fruit and seed growers more effectively than in the past.

Butler (C. G.). — 1952. **The development of British honeybees.** (*Rev. Ass. Agric. Lond.*, **17**, 9.)

A discussion of the development of the strains of honeybees in Britain today, together with some views with regard to their future development.

Butler (C. G.). — 1952. **Behaviour of social insects.** (*Nature, Lond.*, **170**, 642.)

A synopsis of the papers on this subject read during the Belfast meeting of the British Association.

Butler (C. G.), Free (J. B.). — 1952. **The behaviour of worker honeybees at the hive entrance.** (*Behaviour*, **4**, 262.)

Guard bees are not found at the hive entrance unless their colony has been alerted by the presence of robber bees or numbers of bees that have strayed from other colonies or by disturbance of some kind. The degree of alertness exhibited varies under different conditions and with different strains of bees and may be of short or long duration. Intruders are not molested by unalerted colonies. Bees of various ages undertake guard duties and attempt to intercept and inspect other bees on the alighting-board of the hive. They recognise members of their own colony and distinguish them from bees from other colonies very quickly by scent. Robber bees are, however, recognised as such by their actions before the guards can approach and examine them.

On interception the fate of intruders is largely dependent upon their subsequent behaviour. The guards immediately try to sting robbers and will also fight violently with guard bees from other colonies, but very seldom attack other intruders. Many intruders adopt a submissive attitude and exhibit the "displacement activity" of tongue-stropping, sometimes passing into a state of thanatosis. A high proportion of submissive intruders are mauled and dragged away from the hive entrance irrespective of their age; however, those that do succeed in remaining in a strange colony for a few hours become accepted by the bees of that colony.

Butler (C. G.). — 1954. **The World of the Honeybee.** (*Book. New Naturalist Series London, Collins.*)

Butler (C. G.). — 1953. **The present status of beekeeping in Ceylon and possibilities for its future development.** (*Brit. agric. Bull.*, **6** (26), 125.)

Butler (C. G.). — 1953. **A report on the results of an investigation into the possibilities of beekeeping in Ceylon, together with some suggestions for the future development of beekeeping in the Island.** (*Sessional Paper, Government of Ceylon.*)

Butler (C. G.). — 1954. **The method and importance of the recognition by a colony of honeybees** (*A. mellifera*) **of the presence of its queen.** (*Trans. R. ent. Soc. Lond.*, **105**, 11.)

Data are given in support of the theory that bees normally obtain something from their queens which inhibits them from rearing further queens. The results of experiments and observations indicate that a small number of the worker bees of a colony obtain this "queen substance" by licking all parts of the body surface of their queen, and subsequently share it with the other members of their colony. An adequate supply of "queen substance" inhibits worker ovary development as well as the production of new queens. It is suggested that in ants, bees and termites the collection and distribution of "queen substance" is the most important single factor in the maintenance of colony cohesion.

FABERGE (A. C.). — 1943. **Apparatus for recording the number of bees leaving and entering a hive.** (*J. Sci. Inst.*, **20**, 28-31.)

An apparatus giving a continuous record of the number of honeybees leaving and entering a hive is described. Bees pass through a trap, producing electrical impulses. The recording part consists of a magnetic escapement causing a cursor carrying a type figure to travel above the paper. At regular time intervals the position of the cursor is printed, and it is brought back to the zero position. By actual test it was found that the escapement was capable of resolving a pair of impulses 1/11 second apart with certainty; the resolution may be higher.

FREE (J. B.). — 1954. **The behaviour of robber honeybees.** (*Behaviour*, **7**, 233.)

It is shown that the characteristic, hesitant, swaying flight of robber bees is an innate response to the sight of a congestion of bees, either of their own or from another colony, near the hive entrance they wish to enter. When the entrance of a hive is not crowded with bees, robbers will enter without hesitation, even when the hive contains a colony of bees. It is concluded that guard bees quickly recognise would-be robber bees by their characteristic flight behaviour, and subsequently confirm their identity by olfactory examination.

HARRIS (W. V.). — 1954. **Termites from Socotra (Isoptera).** (*Ann. Mag. Nat. Hist. ser.* 12, **7**, 493-497.) — 1954. **Further records of East African Termites-II.** (*Proc. R. Ent. Soc. B*, **23**, 127-137.) — 1954. **The War on White Ants.** (*New Commonwealth*, 1954, 455-459.) — 1954. **Exhibit of** *Apicotermes* **nests.** (*Proc. R. Ent. Soc. C.*, **19**, 35.) — 1954. **Exhibit of** *Reticulitermes flavipes* **from Hamburg.** (*Proc. R. Ent. Soc. C*,. **19**, 44-45.) — 1954. **Termites in Europe.** (*Ent. Mon. Mag.*, **90**, 194-197.) — 1954. **Developments in Termite Research. Rep. VI.** (*Commonwealth Ent. Conf. London*, p. 126-130.) — 1955. **The Prevention of Termite Damage to Buildings.** (*Colonial Building Notes, No.* **26**, 1-6, D. S. I. R. London.) — 1955. **Termites and Forestry.** (*Emp. For. Rev.*, **34**, 160-166.) — 1955. **An American Termite in Imported Timber.** (*Wood*, **20**, 366-367.) — 1955. **Exhibit of living** *Kalotermes* nr. *jouteli* **and preserved** *Zootermopsis augusticollis* **from imported timber.** (*Proc. R. Ent. Soc. C.*, **20**, 36-37.) 1955. **Termites and the Soil.** (*Kevan, Soil Zoology; London, Butterworths*, p. 62-72.)

HASSANEIN (M. H.). — 1951. **The influence of** *Nosema apis* **on the larval honeybee.** (*Ann. Appl. Biol.*, **38**, 844.)

It was found to be impossible to infect the larval honeybee with *Nosema apis*. In colonies suffering from this disease about 15 per cent of the eggs laid failed to result in adults, probably because of inadequate care and feeding.

KALMUS (H.), RIBBANDS (C. R.). — 1952. **The origin of the odours by which honeybees recognise their companions.** (*Proc. roy. Soc. B.*, **140**, 50-59.)

Bees from two colonies were trained to forage from different dishes, placed one yard apart. Their thoraces were distinctly marked. Recruits to the dishes were also distinctly marked, and they were found to be preferentially attracted to the dish visited by members of their own colony.

Recruits were not attracted to the dishes by the sight or sound of their companions.

They were attracted by their distinctive odour. These odours were not inherited, but were produced by changes in the food supply of the colonies. They would develop between queenless halves of colonies.

Uniform and distinguishable colony odours are a consequence of the wide-spread food transmission which takes place amongst the foragers of each colony. Their role in orientation and the defence of the honeybee community is discussed.

KRISHNAMURTI (B.). — 1939. — **A Brief analysis of eleven years (1928-1938) records of scale-hives, at the Rothamsted Bee Laboratory.** (*Bee World*, **20**, 121-123.)

On the assumption that high temperature, long hours of sunshine and low rainfall are desirable for honey production, a rough classification of the weather conditions in the different years was made. This method, although only a rough one, immediately separated out the best years both for weather and honey production. It was found that years of favourable weather conditions appear to be succeeded by unfavourable ones more or less regularly.

MILNE (P.). — 1941. **Wax-moth and bald-headed brood.** (*Bee World*, **23**, 13-14.)

It was observed that larvae of *Achroia grisella* Fabr. are sometimes found lying alongside pupal honeybees contained in cells from which the normal cappings are missing. Masses of faecal pellets of the wax-moth larvae were found adhering to the pupae, many of which developed with deformed limbs. Burrows from cell to cell were observed. The large number of faecal pellets present and the absence of damage to the mid-rib of the comb suggests that the "Bald-headed" appearance is due to the cappings having been eaten away from below by the wax-moth larvae.

MILNE (P. S.). — 1943. **Brood diseases of the honeybee.** (*Ann. Appl. Biol.*, **30**, 191-194.)

A discussion of the pathogenic organisms, etc., responsible for Chalk Brood, American Foul Brood, and European Foul Brood, and the methods by which these diseases are carried from one colony to another. The attempt to control the two Foul Brood diseases by mutual co-operation between beekeepers and the aid of insurance schemes, and latterly by means of legislation, are described.

MILNE (P. S.). — 1943. **The spread of American foul brood.** (*Brit. Bee J.*, **71**, 298-300.)

A discussion, with a diagrammatic representation of eleven ways in which *Bacillus larvae* becomes distributed within a hive of bees, and of ten ways by which the disease spreads from one colony of bees to another.

MILNE (P. S.). — 1945. **Brood diseases in the three counties.** (*Wilts., Hants, and Dorset Beekeepers Federation 1945 Year Book*, 6-11.)

During 1944, 706 apiaries of bees in Wilts., Hants., and Dorset were visited by officers appointed under the Foul Brood Disease of Bees Order, and 2,253 colonies of bees in these apiaries were examined. Foul Brood was found to be present in approximately 1 in 4 of the apiaries visited, and in 1 in 8 of the colonies examined. For England and Wales as a whole the corresponding figures are 1 in 6 and 1 in 14 respectively, based on reports from 52 counties and on inspection of 23,000 colonies of bees in 6,000 apiaries.

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